Linking biodiversity with environmental drivers and pressures in Great Britain

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Abstract

This thesis describes the original and significant development of a hierarchical statistical framework in order to realign fine-scale spatial covariate data. An example of the utilisation of this framework is given within the context of biodiversity modelling.

Biodiversity is of utmost importance to the correct functioning of ecosystems and the provision of services vital to humanity. Understanding of the impacts on biodiversity by environmental drivers and pressures can help appropriate responses to be taken, to mitigate, halt or reverse damage to habitats. Therefore, linking biodiversity measures with explanatory covariates in statistical models can help understand these relationships and the extent to which certain drivers and pressures are responsible for environmental change.

When modelling biodiversity, the scale at which the variables are measured should be considered. Where data are measured at different scales, a situation of misalignment arises. Misaligned data may be subject to measurement error, which can influence the resultant model, if the data are not realigned.

In order to realign covariate data, two transformation approaches can be implemented. The first method is to aggregate the response data to the level of the explanatory covariates. The second method is to downscale the covariate data to the response locations. This realignment process is more complex than aggregation of the response, since it requires the uncertainty estimation of the downscaled covariate predictions. The developed framework has possible further applications in fine-scale uncertainty estimation of model covariates, where the scale at which the covariates are given is coarser than that at which the response data are available.

Chapter 1 provides an introduction to the main issues and challenges in the thesis: biodiversity, data measurement, modelling techniques, scale and data realignment. The three case studies used in the development of the hierarchical framework are also introduced. Data from Loch Leven on underwater plants are analysed in chapter 2. Carabid data from ten rural locations are considered in chapter 3. In the final case study in chapter 4, coverage abundance data from sites the Countryside Survey across Great Britain are modelled. In chapter 5 the data from chapter 4 are used as the impetus; a hierarchical framework for realigning covariate data is developed and a simulation is created in order to assess its performance relative to the non-realigned model.

Chapter 6 provides a summary of the case studies as well as discussion of the main issues and proposals for additional development.

> When standing on an escarpment of hills, gazing across a wide-spreading plain, we do not see each tree, every road that winds from one hamlet to another, all the spires that peep above the green, or count the innumerable fields, but pick out a few outstanding features that appeal to us and so convey to our mind an impression which is more vivid than if one by one we catalogued all that our eyes rested upon.
>
> So it is hopeless to try and represent the great mosaic which forms the countryside. We can but take fragments as they present themselves, odd and disconnected they may be, but perhaps they help us to understand the whole and lead us to find out more for ourselves.

Pulbrook (1926)

> si hortum in bibliotheca habes, deerit nihil.

Cicero (46 BC), in Shackleton Bailey (1977)

Contents

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Declaration

I, IAIN PROCTOR, declare that this thesis titled, 'Linking biodiversity with environmental drivers and pressures in Great Britain' and the work presented in it are my own. This work has not been submitted in any form for another degree or professional qualification.

I confirm that where I have consulted the published work of others, this is always clearly attributed. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.

Excerpts from chapter 2 have been published in Dudley et al. (2012) in Hydrobiologia and from chapter 4 in Proctor et al. (2012) in the proceedings of the International Workshop on Statistical Modelling.

Chapter 1

Introduction

1.1 The importance of biodiversity

The United Kingdom is required by several international conventions to monitor and protect biodiversity, on the understanding that with an increasing global population, increased consumption and decreasing biodiversity, the environment may not be able to supply the goods and services needed by a dependent humanity. The Aichi Biodiversity Targets, agreed by the Convention on Biological Diversity (CBD) in 2010, contain the mission to:

> ... halt the loss of biodiversity in order to ensure that by 2020 ecosystems are resilient and continue to provide essential services, thereby securing the planet's variety of life, and contributing to human well-being, and poverty eradication. (UN Environment Programme, 2010)

The European Union Water Framework Directive (EU WFD) (2000) is another mandate by which the United Kingdom abides, which requires the attainment of "good ecological status" and "good chemical status" standards in all water bodies of the member states of the European Union, by 2015. Aquatic flora and fauna, as they are affected by the chemical status of the water, are used as determinants of the ecological status of the water systems.

In studying the consequences of recorded biodiversity loss, Chapin et al. (2000) conclude that widespread changes in biodiversity and ecosystem services are due to human alteration

of the environment. This view is supported by Hooper et al. (2005) in their review of the effects of biodiversity on ecosystem function, stating that in many well-documented cases, anthropogenic forces have caused species invasions, leading to the alteration of ecosystem functioning and subsequently the alteration of goods and services provided by those ecosystems.

Isbell et al. (2011) assess the importance of plant biodiversity in a meta-analysis of grassland biodiversity experiments, in order to explore the relationship between species richness and ecosystem functions across space and time. It is inferred that although certain species may appear redundant for the promotion of a given ecosystem function at a certain point in time,it may be needed under different climatic conditions or for other functions. Thus a higher level of species richness can aid the stability of an ecosystem by promoting a greater number of functions under more environmental conditions.

Costanza et al. (1997) calculate the value of 17 ecosystem services, such as water regulation, nutrient cycling and food production, vital to the functioning of human welfare, at a minimum of $33 trillion (approximately $50 trillion in 2015). The preservation of biodiversity in many environments is necessary therefore, as ecosystems are reliant upon the diverse array of species in order to deliver the services vital to humanity.

Therefore the recording of biodiversity, underlined by international convention, is of great importance, both as a determinant of ecological status and as integral to further functions of ecosystems and their services. Information is required about the links between biodiversity and environmental drivers of change, in order that good understanding of the relationships and processes between biodiversity and these drivers and pressures be developed. Action can then be taken on anthropogenic drivers, or preventative measures taken to inhibit, halt or reverse the loss of biodiversity in different ecosystems. Understanding of these processes is developed partly via a modelling framework, allowing the changes in biodiversity to be attributed to known environmental changes, in order that appropriate action on the responsible drivers and pressures may be taken.

1.2 DPSIR - a framework

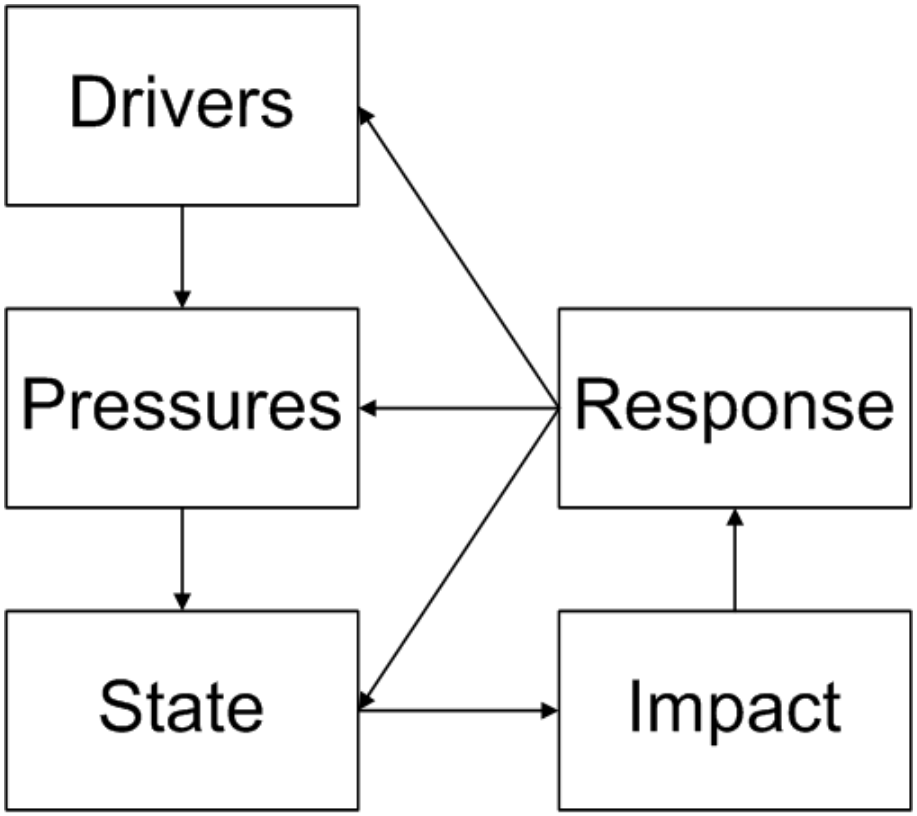

Figure 1.1: An example of the DPSIR framework, as outlined by Gabrielsen and Bosch (2003). The framework is useful in identifying causal linkages in environmental relationships, eliciting a response, possibly in the form of governmental policy to limit or prevent driver and pressure activity, and thus protect the impacted environment.

In order to place environmental data analysis within the context of anthropogenic drivers and governmental regulations, one can use a framework such as **DPSIR** (Driver Pressure State Impact Response). This framework affords the ability to view policy changes for government, industry, private companies and individuals as a response to changes in the state of the environment and impacts on ecosystems. A flow diagram of how this model could be understood can be seen in figure 1.1.

As outlined by the European Environment Agency (2007), the *'drivers'* refer to anthropogenic activity such as industry, agriculture or transport, which affect *'pressures'* such as emissions or effluent which in turn affect the environment. The *'state'* heading covers environmental states, for example: the phosphorus concentration in water, soil moisture, or acid

concentration levels. The *'impact'* on the environment is comprised of effects on biodiversity, for instance increased risk of flooding or drought.

A more socio-economically minded DPSIR model might include tourism or tax revenue in this category; this thesis will not be concerned with these areas here, but rather environmental impacts. The *'response'* is regarded as changes to regulations concerning industrial, farming and private practices. These changes could take the form of preventative laws or taxes on certain drivers to try and mitigate the effect of their respective pressures. Pressures may also be those naturally occurring, such as coastal erosion, but preventative measures can also be taken to combat such activity. Gabrielsen and Bosch (2003) outline the DPSIR framework, by showing how the inferred response from the drivers and pressures is used to refer to other aspects of the process, in order to follow how changes occur along the causal path, and how the policy initiatives will alter the eventual response.

The aforementioned international protocols - the CBD and EU WFD - could be regarded as *'response'* measures. It is worth remarking at this point on the ambiguity of the term, *'response'*. Within the DPSIR model, it does not refer to the dependent variable, but rather policy implemented on *'drivers'* and *'pressures'*. Unless set within quotation marks, the word will be used following statistical understanding of the term from this point, denoting a dependent variable in the analysis.

The position of a parameter of interest within the DPSIR framework is dependent upon whether it is viewed - in statistical terms - as an explanatory or response variable. When looking at the macrophyte data from Loch Leven in chapter 2, for example, we could view lake water quality measures as our explanatory variables and the macrophyte population as the response. Thus, water quality is included as a *'state'* and the macrophyte response is the *'impact'*. Viewing some measure of the water quality as a dependent variable and wet deposition as an explanatory covariate means the water quality is now an *'impact'* and precipitation chemistry is a *'state'*. Also emissions estimates from industrial or agricultural sources may ordinarily be denoted as *'pressures'* in a DPSIR framework, but could be used as explanatory variables within a statistical model.

DPSIR itself is not used in this sense a rigid mechanistic model but a policy tool to view ecological changes in terms of a series of consequences. Whether a variable is treated as

explanatory or response may have implications for how uncertainty within the measurements is treated; measurement error is discussed further in section 1.5.1.

According to figure 1.1, to be able to make informed *'responses'* to *'drivers'* and *'pressures'*, one needs to know how they affect the *'state'* and *'impact'* components, in order to make appropriate policy decisions regarding drivers of change. Inference must be made on the dependency of the *'impact'* variable in question, on certain *'pressures'* or *'state'* factors, in order that an appropriate *'response'* might be enacted. It can be that a dependence relationship is unclear, due to the *'driver'*/*'pressure'*/*'state'* data being inaccurately recorded.

An example of the DPSIR framework in use is in the study by Pirrone et al. (2005) on eutrophication in the Po river catchment in Italy. Using this structure, the study identified agricultural and industrial activity as the causes of nitrogen and phosphorus loads into the river. The report of the RUBICODE (Rationalising Biodiversity Conservation in Dynamic Ecosystems) workshop (2008) used the DPSIR framework in combination with a Social-Ecological System in the assessment of the effect of environmental activity on ecosystem services in seven aggregate ecosystem categories.

In this thesis, the focus is placed on the relationship between the drivers and pressures, the state of the environment and the impact produced. Thus, this thesis will mostly be comprised of analysis surrounding the '**DPSI**' section of DPSIR. The aim of the analysis presented is to link spatio-temporal changes in a biodiversity impact with environmental drivers and pressures. A basic diagram of the model concept is shown in figure 1.2. Thus the dependent variable will be some measure of biodiversity, termed the '*impact*' by the DPSIR framework. The explanatory variables will be covariates of drivers, pressures or states to describe the variability in the biodiversity response.

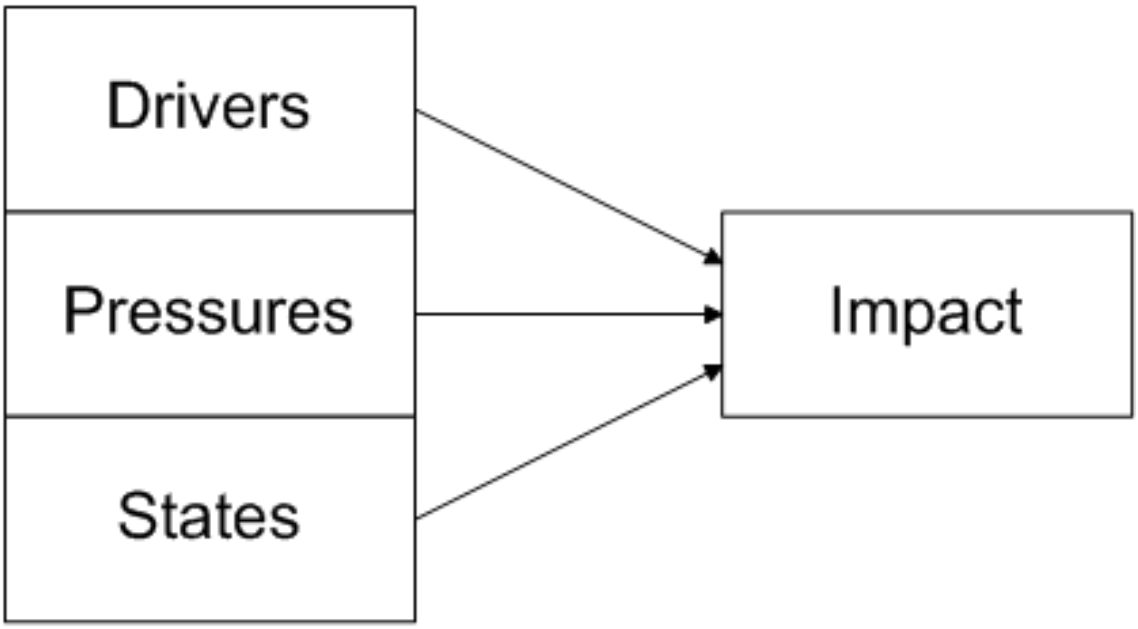

Figure 1.2: An diagram of the modelling concept, linking biodiversity with environmental drivers and pressures by describing variability in the biodiversity impact in terms of driver, pressure and state covariates.

1.3 Measurement

Having stated the importance of biodiversity and the ability to view it as a response to environmental change in a statistical model, some measure of the chosen variables is needed. This section will focus on how the data will be measured. This will be discussed with regard to defined measurement methods. Various methods of measuring biodiversity and different explanatory covariates will be outlined, which will be used in modelling the biodiversity response.

1.3.1 Niches

As previously stated, loss of biodiversity has been linked with the malfunction of ecosystems and their inability to provide vital services. Changes in this variety occur due to changes in the present environmental drivers and pressures. How such changes would occur is understood initially by defining the concept of a species' niche.

The niche concept was put forward by Grinnell (1917) in relating the specific locale of the bird species *Toxostoma redivivum* (California Thrasher) to a narrow range of environmental conditions present in certain regions of the Californian mountains. For a single variable, such as temperature **T**, one may state that the fundamental niche for a certain species consists of an interval $[a,b] \in \mathbb{R}$ such that in a given region if **T** has value t which is outside of the interval, then the species would not be able to survive. In field experiments the fundamental niches of species cannot always easily be measured, as taxa are intrinsically inter-related and therefore the change in some environmental pressure that affects one species will impact upon the wider ecosystem as a whole, in some way. The realised ecological niche was then proposed formally by Hutchinson (1957), who gave grounding for the conditions under which a species may be able to exist, given its competition for resources, and interaction with, other species. It is effectively a hypervolume bounded by the limiting resources necessary for the survival of a determined species in that environment; the realised niche of a certain species is that subspace of the fundamental niche which has the presence of the species within a given environment.

Consider an ecosystem with several species present, which are integral to the delivery of vital services. If the environmental conditions change to a state outside of a present species' realised niche, then it will cease to be able to exist there and the diversity will fall. Thus as exemplified in the review by Hooper et al. (2005), the services provided by that ecosystem may suffer as a result. Thus the more diverse a community is, the more stable the ecosystem will be and its ability to provide the required services will be less under threat.

Even when the conditions are within a certain species' realised niche, it may be difficult for that species to survive, due to the environment being close to the limit of what conditions it can withstand. When conditions enter the realised niche of a species, they are said to be at the leading edge of the niche. When the environment becomes more inhospitable to that species, the conditions enter the trailing edge of the niche.

As the environmental state changes, the conditions may reach the trailing edge of certain species' niches and so become less favourable to their survival. Thus abundance of those species may fall or they may disappear altogether. Conversely, the conditions may enter the leading edge of potentially invasive species on the fringes of that region and become more hospitable to their own survival. Therefore their abundance may increase or previously

absent species may invade the area and so a shift in the relative species' abundance can be witnessed.

A biodiversity measure is a form of inference on the health or state of a community of species. It is a facet of the community structure for a given area at a defined point or period in time. The change in the diversity of a species community is indicative of the altered relative abundances of those species present. By measuring the change in biodiversity over a spatio-temporal range, the variability witnessed can be modelled as a response to recorded or estimated changes in the environmental drivers and pressures.

It is worth remarking at this point on the meaning of the term, 'biodiversity'. A broad definition of biodiversity is the 'variety of life', according to a certain region or taxon grouping. In layman's terms, the concept of high biodiversity might be envisaged by an image of the Amazonian rainforest: the prescence of parrots, frogs, monkeys and jaguars found within a canopy of Mahogany trees and vast undergrowth presenting a wide breadth of colour and taxa. However, biodiversity measures are not subjective opinions concerned with colour or beauty. The objective indices presented in this thesis are measures of the heterogeneity or evenness of a targeted taxon community for a specific region and period of time.

1.3.2 Biodiversity

Having previously discussed how changes in biodiversity occur, it is important to understand how these changes should be measured. This process is contingent on the response which is to be modelled, and how the data were collected. A number of different biodiversity measures will be detailed here. Here, the term 'community' will refer to some subset of species in a given region of interest, such as underwater plants (chapter 2), ground beetles (chapter 3) or all plant species (chapter 4).

Data collected in the field are often recorded by some countable measure, such as: presence-absence or abundance of individuals or biomass. These data are usually grouped according to some taxonomic classification, by their respective genera or species. Weiher et al. (1999) detail how the classification of taxa can be made via functional groups, into which different taxa are aggregated. These groupings could be based on particular specific plant traits or plant strategies. As shown by Tilman et al. (1997), the ability of an ecosystem to provide

services efficiently is related to the functional diversity of that ecosystem. Calculation of functional groups is discussed by Tilman (2000), on the basis of physiological and morphological traits of the species, which influence requirements for resources such as nutrients, light, water and phenological characteristics. Hodgson et al. (1999) show how plant strategies may be estimated from the traits of each species. A method for measuring plant strategy is outlined by Grime (2001), where plants are scored according to their ability to compete for resources, tolerate stressful conditions when nutrients are less available and to take advantage of disturbance. The ability of differing species to exploit different niches of the environment allows them to coexist in the same habitat, and thus allows the ecosystem itself to function more productively.

Having recorded the field data, a list is then obtained for each sampling location, of each specific class recorded and its respective value. Multivariate methods can be used to analyse the data in their present form, in order to show relationships, either within the community itself or in relation to explanatory covariates. These techniques will be discussed further in subsection 1.4.2. For other methods of analysis, a univariate measure of the community is required. Probably the simplest univariate measure of biodiversity is richness, i.e. a measure of how many different groups are recorded. This concept does not take into account the abundance in each group, but purely how heterogeneous the community is. Another basic measure is the total abundance of all groups, i.e. the total of all individuals. This does not take into account how even or heterogenous the community is; it is purely the sample population.

Consider that a measure is desired that takes account of the evenness of the recorded groups, i.e. their relative abundances, but also of the heterogeneity of the community. One such measure which attempts to take account of both these facets is the Shannon-Wiener index. In a community of N groups, the index is:

$$\text{Shannon-Wiener index} = -\sum_{i=1}^{N} p_i \ln p_i \tag{1.1}$$

Here, p_i is the fraction of group i recorded in the community. The index is on the range $[0, \infty)$, taking the value of zero, only when there are less than two groups present. A larger Shannon-

Wiener index value indicates greater evenness and heterogeneity within the community. Analyses in chapters 3 and 4 use the Shannon-Wiener index. Another commonly used index in ecological analysis is Simpson's diversity index, which is on the scale $[0,1]$:

$$\text{Simpson's index} = \sum_{i=1}^{S} \frac{n_i(n_i-1)}{N(N-1)}, \tag{1.2}$$

where n_i is the abundance of species i, N is the sum of all the n_i and S is the number of species present. Simpson's index is so constructed that it is the probability that any two individuals randomly sampled independently from the community will be of the same group. As noted by Pielou (1975) in this form, Simpson's index is not a measure of diversity but of dominance, since larger values of the index are recorded where the community is dominated a small number of species. Where used in this thesis, the so-called, 'Simpson's Index of Diversity' $(1-\text{Simpson's index})$ is used instead, as a greater index value is returned for greater evenness in the community, being less dominated by a few species. This index is more easily related to the other indices, which try to indicate greater heterogeneity and evenness by a greater value. Indices exist which try not to take account of the heterogeneity but only of the evenness of the community. An example of such an index is the E_{var} index proposed by Smith and Wilson (1996), designed to be independent of class richness and calculated as:

$$E_{\text{var}} = 1 - \left[\frac{2}{\pi \arctan\left\{ \sum_{i=1}^{S} \left(\ln n_i - \sum_{j=1}^{S} \ln n_j / S \right)^2 / S \right\}} \right], \tag{1.3}$$

where n_i and n_J are the abundances of species i and j respectively and S is the number of species. The E_{var} index is based on the variance of the log abundance of each group, centred on the mean of these log abundances, on the range $[0,1]$. Both Simpson's index and Smith and Wilson's E_{var} are modelled in chapter 4. As outlined by Magurran (2004), there exists a large number of other methods which try to estimate the diversity of a community, including the reasonably well-known Camargo, Margalef and Bray-Curtis indices.

In comparing a number of diversity estimators, Mouillot and Leprêtre (1999) looked at the accuracy with which Shannon, Simpson, and Camargo's indices reflect changes in a simulated community of species. Shannon's diversity index was found to be the most robust for small to medium taxon sample sizes (up to 50 species). The Simpson index performed the best overall, with the lowest relative bias and RRMSE (Relative Root Mean Squared Error) for samples of up to 100 species.

As well as how the data are collected, the area which is surveyed when the data are recorded is important also. It is a common occurrence that when sampling defined taxa, the larger the sample area that is surveyed, the more taxon groups will be recorded which are present in the population. Rarer groups will have a greater chance of being recorded in a larger region which is sampled with the same intensity as a small region. Comparison of unequally sized sampling regions would therefore give rise to a bias in the biodiversity response. Issues concerning sampling bias are discussed further in chapter 2.

1.3.3 Explanatory covariates

The aforementioned drivers, pressures and states in the DPSIR framework will be the covariates in the model structures. These can be recorded by ground observation, ground measurement or model estimation.

Covariates estimated from model procedures can be calculated either by some form of interpolation on the ground measurements themselves, or derived via a mechanistic model. Smith and Fowler (2001), in creating wet deposition maps of pollutants in the United Kingdom use ground measurements taken from monitoring stations, which are then interpolated using a kriging method. These measurements are used in the estimation of critical load exceedance. Mechanistic models, such as the FRAME (Fine Resolution Atmospheric Multipollutant Exchange) model have been applied to model the spatial distribution of sulphur and nitrogen deposition over the United Kingdom, as shown by Dore et al. (2007). Emissions data from the FRAME model are used in the creation of dry deposition maps, as outlined by Smith et al. (2000). Habitat is also important as a covariate to explain the variability in biodiversity. Habitat can be described as an underlying concept, which can be defined in each region by reference to the physiography, abiotic conditions and land management of that specific region.

As previously stated, the array of species within a community is one of the limiting factors for an ecosystem to be able to provide the goods and services demanded of it by humanity. However, the causes of these spatial or temporal changes are desired to be known. The drivers and pressures of this impacted change must be identified, in order that any preventative action can be undertaken to help protect vulnerable habitats and taxon groups, by mitigating, halting or reversing any damage caused. The use of statistical models can be extremely beneficial in linking environmental drivers and pressures to impacted biodiversity.

1.4 Modelling

Modelling methods and selection procedures will be discussed here, as will the problem of measurement error and data misalignment in analysis. Several methods that deal with misalignment and the specific problems which they attempt to solve will then be outlined.

1.4.1 Ecological models

The following examples describe causal links in the environment, relating impacts to potential drivers and pressures. Using aggregate data from many sites, species response curves can be calculated for single species, identifying conditions they prefer, by inferring from those conditions where their presence or higher abundance is observed. Studies by, for example Wamelink et al. (2005) create such response curves by relating soil pH to the presence of individual plant species. Pakeman et al. (2008) study driver interaction on plant species on South Uist in Scotland. In studying the realised niches for various plant species according to soil pH and soil moisture, they conclude that the realised niches for one environmental covariate can be dependent upon limiting conditions in an another covariate.

Foley et al. (2005) review anthropogenic use of global habitats, subsequent changes and the consequences of such events. It is inferred that due to the degradation of habitats, soil and water sources, biodiversity loss is incurred as a result. Anthropogenic reasons cited for these alterations to the environment include land cover changes, higher nutrient inputs to ecosystems and increased water consumption.

Thuiller et al. (2006) model the effect of anthropogenic climate change on migration of tree species and the resultant changes in diversity across Europe. Using forecasts of climate conditions, losses of both functional and species diversity in central Europe are predicted, along with increases of diversity in extreme regions. As well as occurring over time, observed spatial scale gradients can be used to infer differences in the impact of human activity on the environment. Bobbink et al. (1998) analyse the nitrogen deposition effect on European vegetation, in several different case studies across Europe. Detrimental effects on plant diversity in sensitive systems are shown in various habitats, including freshwater, grassland, heathland and forest environments. Decreases in the diversity of systems due to increased nitrogen inputs are witnessed and also the decrease in biomass of specific species.

In nitrogen addition experiments in North America, Clark et al. (2007) study the species richness response in grassland habitats. Under different input loads of nitrogen, sensitive habitats showed a greater negative response in the plant community. In the analysis conducted, this sensitivity was best characterised by the soil cation exchange capacity, i.e. the capacity of the soil to retain deposited nutrients, in the form of nitrogen molecules.

Using long-term data from the British countryside, Smart et al. (2005) relate changes in trait representation in various habitats to anthropogenic drivers of change. Changes in three surveys from 1978 to 1998 are analysed. Increases in grass species and decreases in stress-tolerating species in plots from the Countryside Survey are inferred to be the result of increased nutrient inputs to the environment due to intensive farming activity. Grazing intensity by livestock is cited as another possible pressure.

Having cited numerous examples of studies where causal links in the environment are described, it is worth mentioning the role of statistical models in this process of understanding such links. Although correlation between covariates and the response can be shown in a statistical model, one cannot infer causality directly from such a relationship. Scientific knowledge is needed to help make such inferences. In light of this, statistical methods used in ecological settings will now be introduced.

1.4.2 Multivariate methods

Having already discussed the measurement of biodiversity to be calculated and the covariate data, a model structure is required. This will allow inference to be made on the relationships between the biodiversity response and the environmental drivers and pressures. One group of statistical models used to model such relationships is that concerned with multivariate analysis. The following techniques are often used as preliminary tools in the analysis of ecological data, to investigate species responses to a variety of possible covariates, which may be included in a further model structure.

With the potential impact of a large number of environmental drivers upon a species assemblage, it is difficult to decide which covariates to include in a regression model. A representation of species' presence or abundance across a gradient can be achieved using varied multivariate techniques. The aim is to reduce the numbers of dimensions of the data - spatially or temporally - while losing as little information from the data as possible. Thus, the result from a multivariate analysis will be comprised of the axes containing the most variability in the data.

Suppose that a list is recorded of the presence or abundance of an ensemble of taxa at different spatio-temporal positions. One of the techniques for modelling the variability is multidimensional scaling (MDS), which returns an ordination based solely on the relative variability between data from different sampled positions. This method is outlined and utilised in the exploratory analysis stage in chapter 2. Inference is made as to the change in the macrophyte community over time, using presence-absence data from the lake surveys.

Other techniques exist, such as Detrended Correspondence Analysis (DCA) as developed by Hill and Gauch (1980), used to detect the main gradients in species community data sets. By using covariate data associated with each location where species are recorded, the association between species and their preferred environment can be analysed. Knut et al. (2003) apply this method to ordinate plant species along environmental gradients, subject to their presence or absence in Norwegian swamp forests. Duckworth et al. (2000) also use DCA in investigating vegetation-environment relationships in calcareous grasslands. In this case, the response sites are ordinated according to different environmental gradients. Temperature, latitude, grazing, land cover and soil matter are shown to be the gradients which best explain the variability between the sites. This idea of ordination was then furthered by Ter Braak

(1987), who developed Canonical Correspondence Analysis, allowing a holistic picture of environmental covariates, sites (or time periods) and species responses. Consider the situation that co-located covariate data are available for the response sites. In this method, the responses from species are constrained to the axes of the measured environmental variables. This direct gradient analysis technique assumes an identical, Gaussian response from all species according to the drivers assessed in the model, which may not be true for the data in question.

These multivariate methods described give only a representation of a higher-dimensional system, and in many cases, do not allow for interactions between covariates to be inserted into the model. The resultant inferences are based on the percentage of variability explained by the dimensions displayed, and these techniques do not return significance values, or specific parameter estimates for the effect of each covariate.

1.4.3 Regression methods

In order to obtain parameter estimates of the relationship between the response and each covariate or interaction term, regression methods can be implemented. In regressing the biodiversity response as a univariate measure against chosen covariates, a method of expressing how well the covariates describe the variability in the response structure is needed. Several regression methods are outlined in this section, with examples of their application to real data.

An initial method of modelling a biodiversity response could be with a GLM (Generalised Linear Model) structure; this is outlined in chapter 2. This model structure is relatively well-known and used widely in ecological contexts, as discussed by Bolker et al. (2008) and Guisan et al. (2002).

The MARS (Multivariate Adpative Regression Splines) method, as developed by Friedman (1991), uses the products of one or more hinge functions of the model covariates to describe the variability in the response. The MARS structure starts from the position that given covariates $\mathbf{x} = (x_1, \ldots, x_n)$, the regression function, $f(\mathbf{x})$ is composed to model the responses $\mathbf{y}$, as follows:

$$\mathbf{y} = f(\mathbf{x}) = \sum_{i=1}^{N} c_i B_i(\mathbf{x}) \tag{1.4}$$

Here the c_i are constant terms, and the basis functions, B_i are defined to be one of the following:

1. A constant term
2. A hinge function of the form $\max(K, x_i)$ or $\min(K, x_i)$, where K is a constant.
3. A product of two or more hinge functions

The model-fitting process is subject to a penalty term, which determines the flexibility of the resultant fitted model. Given the piece-wise format of the resultant MARS models, this method is well-suited to species distribution models, which seek to estimate the ecological niches of certain taxa, as described by Hutchinson (1957). Leathwick et al. (2005) use this method in order to predict the distribution of freshwater fish species.

The Generalised Additive Model (GAM) structure is a method of expressing the relationship between the covariates and the response through the use of smoothing splines. This allows for a smooth trend to express the relationship between the response and each model term. The initial setup for the GAM structure is similar to equation 1.4. Here the response is fitted using splines; each spline $s_i(X_i)$ is the function of a covariate, X_i. The function $s_i(\cdot)$ is the sum of a finite number of basis functions; bivariate splines can be fitted also. GAM structures usually use a penalty term in the fitting process, to control the flexibility of the regression splines computed. The calculation and fitting of GAMs have been developed by Wood (2000, 2004). This regression model structure is utilised in chapter 4.

The advantage of the GAM structure is that it is a more natural extension of the GLM structure than the MARS method. As is shown by Guisan et al. (2002), GLMs may be seen as constrained GAM structures. Whereas MARS limits the range of influence of each term in the model via the hinge function, the GAM method relaxes the condition on the spline shape,

and produces a continuously differentiable regression line for each model term. GLM and GAM structures can both easily be modified to incorporate random effects also, which allow for the estimation of the within and between group variability. Methods for GL(M)Ms (Generalised Linear (Mixed) Models) and GA(M)Ms (Generalised Additive (Mixed) Models) are described in detail in chapters 2 and 4 respectively.

GAMM structures are used widely in analysing ecological data also, and model performance in the context of spatial data as studied by Beale et al. (2010) is shown to be comparable with other methods such as Bayesian Conditional Autoregressive and Simultaneous Autoregressive models.

Rowe et al. (2011) use all three of the aforementioned methods in their single species analyses, in order to analyse species' ecological niches across the country. The resultant fitted models using GLM, GAM and MARS structures are combined in order to produce an ensemble forecast of habitat suitability based on the mean Ellenberg N score of the co-occurring taxa. Ellenberg values are arbitrary point estimates ascribed to each plant species on each of several scales, based on the preferred environmental conditions under which each species tends to be found. The name, 'N score' refers to the point estimate of soil fertility in which a given species is found. If a species is usually found in very fertile, nitrogen-rich soils, it would have a high fertility Ellenberg value. Conversely, if it were found more commonly in low fertility soils, it would have a relatively lower fertility value. Other Ellenberg scales defined for the British countryside by Hill et al. (1999) are those of light (L), moisture (F), temperature (T), soil or water pH level (R) and salt content (S).

Indicator values are rather elegant and simplistic, enabling a quick summation of several environmental factors, and thus allowing important drivers to be identified, without the need for time-consuming atmospheric chemistry and soil samples to be taken, which themselves may be subject to large fluctuations over time (Diekmann, 2003). When considered with the aid of the **DPSIR** framework, the 'state' of the environment is inferred from the species that can be found there, i.e. the 'impact'.

The argument for the validation of Ellenberg values by using actual field measurements has several reasons. Firstly, Ellenberg values are based on an arbitrary system, and do not correspond directly to a proportional physical scale. Secondly, Ellenberg values were created

using expert judgement, and taking measurements allows the adherence of an indicative system to estimated covariate data. Thirdly, the Ellenberg system is based on point estimates of a species' optimum conditions for growth, which gives no basis for the range of possible conditions for existence. An understanding of an interval-based system of a specific plant's niche would be more appropriate for the prediction of community composition change. Wamelink et al. (2005) use smoothing splines to describe the responses of over 500 individual floral species, by using the measured soil pH as a covariate term, in order to evaluate the validity of Ellenberg N scores for plant species present in Dutch habitats.

Other non-regression methods include envelope-based approaches, so-called 'dynamic models', for example composed by de Vries et al. (2010), generalized dissimilarity modelling, applied by Ferrier et al. (2007) to model diversity between habitats, neural networks, e.g. in analysis by Olden et al. (2006) and many applications of Bayesian models, for instance as discussed by Wikle (2003).

1.5 Scale

In the use of multivariate and regression methods, data may be obtained from various sources. One difficulty incurred when interpreting statistics from a range of sources is that of scale. When interpreting results, they must be viewed in the context of the scale which was used in the survey. Scale is a combination of two different measures: *extent* and *grain*. The extent of the sampled data or modelled estimates denotes the size of the region over which the data are assembled; the grain is the grade with which data over the survey region are sampled or modelled; the measure of the region mesh. The difficulty arises in creating a viable sampling strategy to obtain sufficient data. When using a 'fine' grain, biotic forces may obscure atmospheric pressures. Conversely, in a review of plant population modelling, at a 'coarser' grain, biological factors may be lost. A trade-off is necessary, as discussed by Jeltsch et al. (2008), between having a fine enough resolution to model ecological processes while at the same time creating a general model for the broad spatial scale. One must be careful also to make sure that inferences made on the resultant model obtained from the fitting process must be made with regard to the scale at which the data were modelled.

When aligning covariate data with the response, it may not be sufficient to assume that the response is nested within a coarsely scaled covariate measurement. For instance, consider that a region of interest has a single covariate value associated with it, while the area is also composed of subregions; the response variable is recorded at this finer subregion resolution. If the covariate in question is considered uniform in its distribution, then one does not need to alter the covariate values, since the covariate value can be assumed to be constant across the region. However, if the covariate is considered to vary across the region, the modelled value will differ with respect to the true distribution of the covariate. Vegetation surveys, for instance, are located at specific points within small regions of 1km^2. In order to understand the effects of atmospheric deposition at such specific locations, deposition data values need to be associated with each response location.

Deposition maps for instance, are subject to measurement error; pollutants do not fall uniformly over each grid square. That is, the modelled estimate is not constant over its respective region. Rainfall data from the Met. Office is also subject to uncertainty in the interpolation process, as mentioned by Dore et al. (2007). The difference between the estimated value for the square and the true value at the response location is the error. A formal description of this error structure is given below.

1.5.1 Measurement error

Measurement error is the name given to the difference between the measured value and the true value of the covariate that is wished to be known. Given covariate data containing measurement error, how does one satisfactorily incorporate it into the analysis? Explanatory covariates in a model often contain error within them, if the data are hard to collect or if precise measurements are not possible. Taking this error into account can allow us to obtain a more valid statistical model, and thus a better understanding of the relationship between the covariates. The potential danger with environmental data is that a large measurement error is present in the measured or modelled variables, thereby causing a false interpretation of the true underlying effects. Depending on the nature of the error structure, this can lead to an actual effect becoming unnoticed, an artificial relationship becoming significant, a negative relationship being interpreted as positive, or vice versa.

To start understanding measurement error, one can take a general situation for further application. We have a response variable Y, which we seek to model in terms of our explanatory

variable, X. The values of X are true, but they have not been observed; W has been observed in place of X. Association between X and W can be expressed basically in one of two ways, using classical or Berkson error. The classical measurement error approach, as described by Carroll *et al.* (2006) is;

$$W = X + U_C \tag{1.5}$$

where $E(U_C|X) = 0$ Carroll et al. (2006). Within the context of data collection, classical measurement can be understood as instrumental error. For instance, air quality measurements may have a quantifiable degree of inaccuracy in their readings. For a given sampled site, i, what is recorded from the machine is the W_i value, and the true X_i is obscured from view. The error term U_C can be estimated in a variety of ways, such as by calibrating W against true values of X, as described by Gryparis et al. (2009).

Berkson measurement error is caused by a different situation. Consider a grid square in which a site is positioned. Suppose that its associated value is valid as a mean estimate for the grid square, but we do not possess information on the true distribution of the covariate across the region of the square. The true distribution of the independent variable of interest, X is not available. Such an example can be seen in chemistry and weather data. When measuring an atmospheric input at a single location, it is not possible to know the value of the variable across the rest of the region of interest (at any grain level). Therefore, there is a recorded variable W, which is a surrogate of the unknown X. This is termed a form of Berkson measurement error, in that the modelled variable W alters from the underlying, true variable, X. The relationship between W and X can expressed as follows:

$$X = W + U_B, \tag{1.6}$$

where $E(U_B|W) = 0$; thus $E(X|W) = W$. This relationship is called Berkson error, as discussed by Berkson (1950). It is this underlying U_B in equation 1.6 that we seek to model. In the case of biogeochemical or meteorological data in chapter 4, the W observed measures are modelled at the centroid of a grid square and the 'true' measure, X, varies spatially within the grid square. For the data in chapter 4, the Berkson error model is more appropriate; these errors are dependent on the variability of the modelled environmental measurement over the area of interest. The Berkson error would be dependent upon a wide range of factors, and so would need to be calculated specifically for each site.

The U_C error term is the error in measuring the variable W instead of the true X variable. The U_B error term is the uncertainty associated with W, when estimating the value of X, given the value of W. Where both classical and Berkson measurement error exist in the data, two errors can be combined into one model, resulting in the following equation:

$$X + U_C = W + U_B \tag{1.7}$$

The importance of error variance is linked to model power, with respect to hypothesis testing. Koul and Song (2008) have shown that power decreases as the Berkson error variance increases. A large amount of literature is available in this area of study, including epidemiological studies by Sheppard et al. (2011) and Gryparis et al. (2009).

1.6 Realignment techniques

Gridded covariate data **W** can be assumed to be valid values of the underlying **X** variable for their respective regions. Thus, for any point in a grid square i, $X_i = W_i$. For a given point k within the square i, the estimate of X_{ik} is $E(X_{ik}) = W_i + U_{B_{ik}}$, where $U_{B_{ik}}$ is the Berkson error term associated with location k in i, given W_i.

Given the presence of Berkson measurement error in gridded covariate data, how can the value of the covariates be predicted accurately at new locations within the region, whilst also taking account of the uncertainty in the modelled areal data? A prior model of some environmental variables may be needed before they can be inserted into the biodiversity response model. Due to the potential of Berkson error in the covariate data, estimation of the uncertainty may need to be made; an in-depth approach is therefore required. Improved understanding of the intra-square uncertainty for the modelled covariates is desired, in order to estimate the covariate values at the finer scale.

Various methodologies have been developed to evaluate the distribution of a meteorological or biogeochemical variable of interest, whose value is only given for blocks or certain points across the whole region under analysis. What is often desired is the estimation of the variable at a new set of points or regions. This problem may present itself in many different ways. It may be required that, given known values of the covariate at one set of points, the variable is to be predicted at a new set of points. There may be new blocks to be estimated, which are nested within regions which have covariate estimates assigned to them. It may also be the case that block estimations are required from point data or vice versa. When there is a spatial or temporal discrepancy between the position of covariates and the response, this is termed, 'misalignment'.

Such procedures as kriging, interpolated distance weighting (IDW) and neural networks may be used to interpolate the data given. Covariance structures are imposed upon the data in many models along with prior estimates of the nugget, sill and range parameters. Attorre et al. (2007) compare these methods for interpolating different environmental variables across the United Kingdom, with kriging returning the best results for the majority of variables tested. Bowman et al. (2009) model the spatio-temporal distribution of sulphur dioxide deposition across Europe using a developed additive model structure and data from irregularly spaced observation sites, allowing the simultaneous description of spatial and temporal patterns.

Ground measurement data and modelled emissions data, sometimes used on their own for deposition analysis can be utilised together to create a more accurate picture of deposition. Fuentes and Raftery (2005) use data from measured sites and modelled areal estimates to form new prediction maps of sulphur dioxide for the eastern United States. Using these sources of information with different spatial resolutions, they are both assumed to be based on a latent spatial process. The measured site data are subject to classical measurement

error, and additive and multiplicative biases are included in the modelled areal estimates. The process is modelled as locally stationary and isotropic, by parameters that are allowed to vary across the region, thereby accounting for the lack of stationarity of the whole process. Sahu et al. (2010) investigate a similar problem in modelling the wet deposition of sulphates and nitrates for the Eastern U.S., also by incorporating a measurement error structure to relate block estimations to point measurements. Where deposition ground measurements are not available to use in conjunction with modelled grid values to produce prediction maps, such approaches are not suitable.

Information from map data can also be used to inform the modelling of environmental covariates. Daly et al. (1994) state the orographic effect upon weather effects in many parts of the globe, and that a local relationship can be formed between precipitation and altitude. Weather station data from across the United States and gridded altitude data are used to create a precipitation map on a 6×9 kilometre grid; prediction intervals for the predicted block data are also calculated.

1.6.1 Downscaling

The concept of downscaling is the re-estimation of coarsely-scaled data, often from a regional or global climate model to a finer-scale, over a spatio-temporal scale. Often these methods are implemented on data from Global Climate Models, in order to evaluate data at a finer resolution for given output from a previous model. These methods typically involve predicting the value of a variable at the 10km grid square level from 100km gridded data. Statistical downscaling involves the calibration of the variable which is to be downscaled, to measured data via a regression model, then predicting the downscaled value at the subregion level, taking remaining error into account. Berrocal et al. (2009, 2010) use data from measurement networks and modelled data from a 36km^2 grid in developing a bivariate model to downscale spatio-temporal ozone and particulate matter data in the Eastern US.

1.6.2 Hierarchical structures

Maraun et al. (2010) review various methods used for downscaling data from regional climate models and the ability of these methods to meet the needs of the ‘end user’. Output from downscaling methods is not usually the eventual end of the process; often the data are

required by policy makers or impact modellers, to implement them in further model structures. One of the needs of some end users is knowledge of the extent of the uncertainty of the downscaled data. A hierarchical model structure can be implemented, where the uncertainty, calculated in the initial stage in the structure, is carried through to the modelling of the response variable. Examples are given below of processes modelling environmental impacts in terms of biogeochemical or meteorological data.

This process of realigning or downscaling covariates for use in a hierarchical model is used, for example in some epidemiological studies to analyse hospital intakes as a response to changes in the concentration of a certain atmospheric pollutant. Zhu and Carlin (2000) use a Bayesian spatio-temporal model with nested misalignment to look at how traffic density affects asthma hospitalizations in California. Misalignment in this case is allowed to occur across years as well as spatially.

Zhu et al. (2003) modelled the ER visits for asthma-related hospitalisations in Atlanta, Georgia with ambient ozone level data as an explanatory covariate. Ozone in this example is measured as a point process across the region, with the response being recorded at the zip code level. This is denoted a 'change of support problem', outlined by Gelfand et al. (2001), due to the response and explanatory variables being measured at area and point levels respectively. This model uses a complex Gibbs sampler, involving twelve parameters to be drawn from the full conditional distribution and a separable space-time covariance structure.

A simulated scenario involving classical measurement error in climate data at the fine-scale level is created by McInerney and Purves (2011) with a framework developed for use in species distribution models (SDMs). It is noted that rarely do SDMs take local scale uncertainty into account, particularly in the context of possible Berkson error in environmental covariates. Covariate data at such a fine scale are rarely collected over broad regions, whereas flora and fauna surveys *are* carried out at such a scale. Such uncertainty, although not often considered, is important in the modelling of biodiversity data, in order that correct inference be made as to the causes of environmental impacts.

1.7 Model framework development

As shown in the epidemiological models above, the misaligned pollution data can be incorporated into a hierarchical model structure, for use in describing the variability in the hospital admissions response. In this thesis, the response variable of interest is the biodiversity response.

The structure of data lends itself to a hierarchical model set up, where the uncertainty in downscaled biogeochemical and meteorological covariates can be carried through to the eventual modelling of the biodiversity response. What is required is a downscaling framework, whereby the measurement error in the gridded environmental data is estimated. Standard downscaling methods are unsuitable, since there is no information available on the covariate distribution within the grid square, and no automatic sub-regional information with which to calibrate the coarse covariate data. With reference to the Berkson measurement error structure, where W is measured in place of X, the relationship $X = W + U$ is recalled. With no immediate knowledge of the distribution of U, the significance of the covariate X may be inaccurate, given W is used in its place in the model. The response location k is in a grid square i, has value W_i. What is needed is a realigned prediction of W_{ik} at the response location k, given the value of W_i. The uncertainty in this realigned prediction also needs to be taken into account, which is termed U_{ik}. The distribution of U_{ik} is dependent upon the prediction of W_{ik}. The downscaled value of X_{ik} at the response location is therefore $X_{ik} = W_{ik} + U_{ik}$.

In practice, this framework is used to downscale gridded biogeochemical and meteorological covariate data to the spatial location where the biodiversity response is sampled. This is conducted by using the value of a given single covariate in the surrounding grid squares, and regressing these values against altitude data to obtain a trend. This trend is then used to predict the covariate value at the finer-scale sampling position. By associating a prediction distribution for U_{ik} with each new predicted covariate value W_{ik}, repeated samples of the covariates can be produced by re-sampling the error terms from their respective prediction distributions. Summary statistics of the output from all models can be used to assess any potential change in the relationship between the downscaled explanatory and response covariates.

1.7.1 Model fitting and selection

There are several ways of fitting regression models, the best-known of which is the Least Squares Estimation. Other methods include Maximum Likelihood Estimation (MLE), Restricted Maximum Likelihood (REML) and Iteratively-Reweighted Least Squares (IRLS). Maximum Likelihood is consistent in its estimate of the parameters, but Wood (2006) describes how ML produces biased model variance estimates, given a large number of model parameters and a small dataset. Choice of these model-fitting criteria will be discussed later in the thesis.

In comparing two fitted models with the same response, a method of choosing which model is most appropriate is sought. Therefore a process is needed to decide which covariates and interactions should be in the model, and the criteria each model will be tested against. For the regression model selection process, there are differing models to be chosen between, with covariates fitted either as singular or joint smoothers (in an additive model), and also as linear variables. The model are fitted, and the results are produced. Coefficients are obtained for each of the linear variables and p-values for each smoother and linear covariate, in the same manner as for the linear models. Criteria for model selection are therefore needed at this stage.

Akaike's Information Criterion

In its most general sense, Akaike's Information Criterion (AIC) as developed by Akaike (1974), is not a measure of whether a model is valid or not, as weighed up against a hypothesis test, but a selection criterion between any number of models for the same response. In its simplest form, AIC is:

$$AIC = 2k - 2\log(L), \tag{1.8}$$

where k is the number of model parameters and L is the maximised likelihood function. This statistic is a relative measure, for use in comparing models against one another; it cannot

be used to test the validity of single models. A lower AIC value is desirable, as a larger likelihood value relative to fewer parameters is the desired effect. Throughout this thesis the AICc, proposed by Hurvich and Tsai (1989) will be used. This criterion is a modified version of the AIC, with a correction term for small sample sizes:

$$AICc = 2k - 2\log(L) + \frac{2k(k-1)}{n-k-1}, \tag{1.9}$$

where n is the sample size and k and L are as in equation 1.8. As n tends to infinity, the correction term tends to zero, and the AICc value will tend towards the AIC value. In this regard, the AICc can be used in place of the AIC for all model selections.

Deviance

For ordinary linear models, the residual sum of squares gives a measure of how much variability exists in the data that is not predicted by the model. Within the context of generalised models, a similar concept is that of deviance. This measure is proportional to how much the log-likelihood of the fitted model differs from the maximum possible likelihood given the data. It is calculated thus:

$$D = 2\left[l\left(\hat{\theta}_{max}\right) - l\left(\hat{\theta}\right)\right]\phi, \tag{1.10}$$

where θ is the vector of all model parameters, $\hat{\theta}_{max}$ is the maximally parameterised model, $l(\theta)$ is the log-likelihood ϕ is the variance. Thus, a smaller likelihood for a certain model will result in a larger deviance. The percentage of deviance explained by a given model is calculated firstly by calculating the maximum deviance possible, i.e. the deviance for the null model. Given a simple linear model structure with response $\mathbf{y}$ and covariates $x_1, \ldots, x_n$, the null and fitted models are constructed:

$$m_1 : \ y_i = \alpha + \varepsilon_i$$
$$m_2 : \ y = \alpha + \mathbf{X}\beta + \varepsilon_i$$

with model m_2 fitted as a function of the fixed effects $x_1, \ldots, x_n$. An intercept term α is fitted and normally distributed error terms ε_i in both models. We let D_m denote the deviance for the model m. The percentage of deviance explained is calculated as $100 \times (D_{m1} - D_{m2}) / D_{m1}$. One can consider the value, $(D_{m1} - D_{m2}) / D_{m1}$ as a generalisation of the R^2 value in ordinary linear modelling. The deviance explained does not penalise a particular model for the number of model parameters included.

The use of the deviance explained as a method of comparing two models based on different responses is indicative of the 'goodness of fit' of the respective structures. However, given the initial difference in variability of the two model responses, comparison of the deviance explained by each model cannot be used to infer which model is better absolutely.

1.7.2 Selection process

Having fitted a model, the choice of covariates and interactions terms may be improved, either by the removal or addition of model terms.

Forward model selection is made by beginning with the simplest model and adding terms; after each term added, the model is re-fitted and then compared with the previous, simpler model. The model will only become more complex in its structure at each stage. The 'full model' is not seen by the fitting process, only the next possible specification.

The process of backward model selection is as follows: the model covariates are inserted into the framework in the desired fashion. It is important to recognise that the model can only get simpler from this initial position, so the variables are inserted into the model in conceivably the most complex, yet still sensible, model possible, given the limits of the model structure itself. A second model is then calculated, which is in some way simpler in form than the initial model. For instance, a interaction term may be removed, or a covariate may be removed from the model completely. This choice of alteration will be dependent

upon which covariate, according to the results of the model, is suspect to not being useful in an explanatory sense, or over-flexible.

Backward selection has the potential to produce a model better-fitted to the data, but less generalised to receive new covariate data for prediction. As the models used in this thesis are descriptive in format rather than predictive, this process of backward selection is common to the fitting of all regression models in this thesis.

In this thesis, the AICc value is used as the selection criterion. Simpler models are compared in turn against the current model of choice. The model with the lower AICc is chosen in preference, and simplifications of that model are then fitted and compared against it.

The AICc score provides a defined process for model selection. A particular model will be chosen in this step-wise manner, thus allowing inference to be made from the resultant model choice as to the usefulness of the remaining covariates. Initially, the choice of model is the most complex model conceivable, containing all covariates and interactions between them. From this position, interactions and the covariates themselves can be removed from the model, pending their lack of benefit to the model fit.

1.8 Aim of the thesis

The aim of this thesis is to develop statistical frameworks to allow the linkage of environmental drivers and pressures and biodiversity responses in the United Kingdom. A variety of habitats and taxon groups will be analysed, in order to try and answer the following questions:

- What evidence is there about how biodiversity in specific communities is impacted by certain environmental drivers and pressures?
- To what extent are these specific communities driven by environmental change?

- How is fine-scale misalignment between the model covariates and the response in the environments best dealt with?

- How can the uncertainty in fine-scale model covariates be estimated?

These questions stated will only be investigated via the analysis of the case studies presented. Thus, the inferences offered in response to these questions can only be made in light of the analyses conducted in this thesis. In all three case studies, the model framework can be considered as a subset of the **DPSIR** framework: the 'impact' is considered as a biodiversity index, which is subject to the effects of 'drivers' and 'pressures'. Differences in scale between potential drivers and pressures and the biodiversity response will be studied, and solutions developed in order to deal with these misalignments. These solutions will be concerned with the optimal methods for calculating the biodiversity response, as well as how to realign the covariate data.

In the course of the analyses, a hierarchical model framework will be developed, to allow the downscaling of model covariates. This will allow the fine-scale uncertainty of these covariates will be estimated. Thus, comparisons can be made between the resultant models, both downscaled and non-downscaled, and inference can be made on the change in the relationship between the model pressures and impact. Assessment can be made as to the effect of certain environmental drivers and pressures on the biodiversity in the communities under analysis.

1.9 Case studies

Before presenting the detailed investigations, a short summary of each of the case studies in the thesis will be outlined.

1.9.1 Macrophytes

Loch Leven, a shallow lake in the east of Scotland is the location in which the first case study is based. Here, the water-dwelling macrophyte (*Macrophyta*) population is the response of interest. Since the beginning of the 20th century, surveys of the macrophytes in Loch Leven have taken place intermittently, but the surveys used have developed in format and methodology over time. Moreover, the sampling methods have not been always recorded precisely. The macrophyte data generally have a small extent but a fine grain. However, this fine grain structure is not replicated in each survey. The locations sampled are not always common between surveys either.

The first response used is species presence, analysed initially using a classical multidimensional scaling approach, which is then aggregated to be a univariate response. Two different scales of response are modelled: the taxon richness of the whole lake and also of separate lake sectors. Covariate data used in these models are: total phosphorus load (mg m^{-2}) and the maximum growing depth (MGD, metres) of the macrophytes in the corresponding year of survey. Phosphorus is used, as it is a potential limiting nutrient of macrophyte growth. It enters the lake from the surrounding agricultural, urban and industrial sources. MGD is considered a surrogate measure of the present lake condition. The sampling sector and the survey year itself are also inserted into the model. Given the turbidity of the lake system and the lack of precise knowledge of the sampling locations, spatial realignment techniques are not used on the covariates. For the years of survey where the sector position in the lake of each sample is known, GLM and GLMM structures are used to model the data, with year and sector within year inserted as random effects and a correlation structure is used to estimate the spatial correlation between the GLM and GLMM residuals respectively.

1.9.2 Carabids

Communities of carabids (*Carabidae*, ground beetles) in rural habitats are profiled in the second case study. The data are taken from transects of ten traps, positioned in different habitats, from ten sites across Great Britain. The carabids are removed fortnightly from these traps, from Spring to Autumn each year. There are usually three long-term transects at each site. Given the differing suitability of each environment to the various beetle species, the numbers of beetles trapped in each trap and transect can vary greatly. Therefore, different spatio-temporal aggregations of the data are used as the response. The data are aggregated by

transect and month; the responses of Shannon-Wiener index and log total of beetles caught are analysed and compared. Since the trap locations are precise and remain in the same position between years and sampling methodology is identical between sites, it is possible to aggregate the response data in this manner.

The covariate data used here are: rain (mm, total per month), temperature (°C, mean per month), wind ($m\,s^{-1}$, mean per month), nitrate-nitrogen and sulphate-sulphur deposition (both $mg\,l^{-1}$, total per month) at each site, as well as year and month of sampling. Univariate indices of log total of individuals and the Shannon index are chosen in order that all taxa are included in a community response. GLMMs with a Gaussian family are used as the model structures here. Exploratory models of all ten sites are fitted, before models of data from two very different sites are compared. Multi-site models are fitted using the same framework and diversity measures of the aggregated response. Year, Site and Transect are inserted as nested random effects into the model where appropriate and an AR(1) structure is implemented to estimate the within-group correlation between successive samples in the same transect.

1.9.3 Plant biodiversity and environmental pressures

In the final case study, data sampled from plant communities in rural habitats across Great Britain are taken from the Countryside Survey (CS) as the response variable. These data are sampled only every 8 to 9 years, but very comprehensively when the survey is conducted. Over 500 sampling sites are used in this analysis. The response data used are the estimated coverage of each floral species within each randomly positioned sampling plot. This coverage is treated as a surrogate abundance measure. These abundances are then converted into a biodiversity index, which is used as the biodiversity model response. Four different indices are tested in preliminary models. Data from the 1990, 1998 and 2007 surveys are used in this analysis.

The covariates in this analysis are: rainfall ($mm\,y^{-1}$), nitrogen deposition ($kg\,ha^{-1}y^{-1}$), altitude (m), easting and northing (km) and plot habitat. Here initially, additive models and additive mixed models are used to model the plant biodiversity.

1.9.4 Data realignment

However, the Countryside Survey data have a large extent and a local fine grain, giving scope for the development of a more complex, hierarchical spatial model structure. Environmental covariate data, which are available at a coarser scale than the CS plot locations, can be separately realigned to the sampling plot level. A method of downscaling rainfall and nitrogen gridded values is developed using altitude as a local predictor variable, in which the newly realigned values also have an additive randomly sampled error term added to them, in order to account for the spatial uncertainty in the newly-predicted values. A simulation study is conducted to estimate the strength of correlation between rainfall and altitude necessary for using this method. The potential of the method to improve model performance with the CS data available is assessed in light of this study.

1.10 Summary

The importance of biodiversity as integral to ecosystem function has been outlined, as has the need for greater understanding of the environmental drivers and pressures which impact upon biodiversity. Statistical methods used in the analysis of ecological and spatio-temporal data have also been discussed. Thus, models will be developed which describe the variability in the biodiversity of different species communities. Spatio-temporal changes in these species communities will then be linked to change in environmental drivers and pressures, at different spatial and temporal scales. The potential of a downscaling methodology to downscale specified environmental covariates will be explored within the context of a hierarchical model simulation.

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Chapter 2

Macrophytes

2.1 Introduction

This chapter focusses on the macrophyte community Loch Leven, in Scotland. It aims to to assess the relationships between environmental pressures and the macrophyte response as measured by taxon richness. Different regression models will be used to assess these relationships.

Lakes have the capacity to provide habitat for a wide variety of different taxa; both flora and fauna. Amphibians, fish, wildfowl, and plants both sub- and semi-aqueous can be found within these systems. The biodiversity of such taxon groups can be used to make inference on the condition of the lake system. Loch Leven is a shallow lake in Scotland which has been used for fishing and water provision over the last century; there are records of the changes in lake condition and biodiversity over time, which will form the basis of this chapter.

The Water Framework Directive (2000) gives guidelines for the condition of lakes and streams throughout the European Union. Lake condition has been inferred from the macrophyte population widely, e.g. by Schaumburg et al. (2004). Such inference can be made through the use of reference lakes, where the trophic status is said to be known. Given a range of reference locations across the range of trophic states, a relationship between the macrophyte communities observed and the stated trophic state can be inferred. Schaumburg et al. (2004) use data from about 100 lakes in Germany, predominantly in the north and west.

The lakes were split into three categories, based on the species that are observed there and identified as being good quality, indifferent or indicative of degraded lake condition. Macrophytes are aquatic plants, which can be found in shallow lakes and lake edges across Great Britain. The response of the macrophyte community can be assessed with regard to environmental drivers and pressures, e.g. the total phosphorus load entering the lake. In Loch Leven the macrophyte population has been surveyed comprehensively several times and shifts in the community dynamic have been recorded. The relationships between potential drivers and the macrophyte response can help give an indication as to the reasons for the recorded change in the macrophyte community. In turn, these inferences may aid predictions for what will happen in the future as a result of changes in the drivers and pressures.

2.1.1 Basics of eutrophication

Ecosystems such as Loch Leven can be classified according to their trophic status, an indicative classification of the diversity and strategy of flora and fauna in the system. The primary determinants of a system's trophic status are biologically useful nutrients, such as nitrogen or phosphorus. Figure 2.1 illustrates a diagrammatic link between nutrients and macrophyte species richness in an ecosystem. The relationship between the nutrient level in a lake and the species richnessis considered to be non-linear. A lake is considered oligotrophic when both nutrient levels and species richness are low. Slow-growing, stress-tolerant macrophyte species tend to dominate their community in these conditions. Mesotrophic conditions occur when nutrient levels are higher and species richness is at its peak. Eutrophication occurs when nutrient levels are higher still and the species richness of macrophytes starts to decrease, with fast-growing, competitive species tending to dominate.

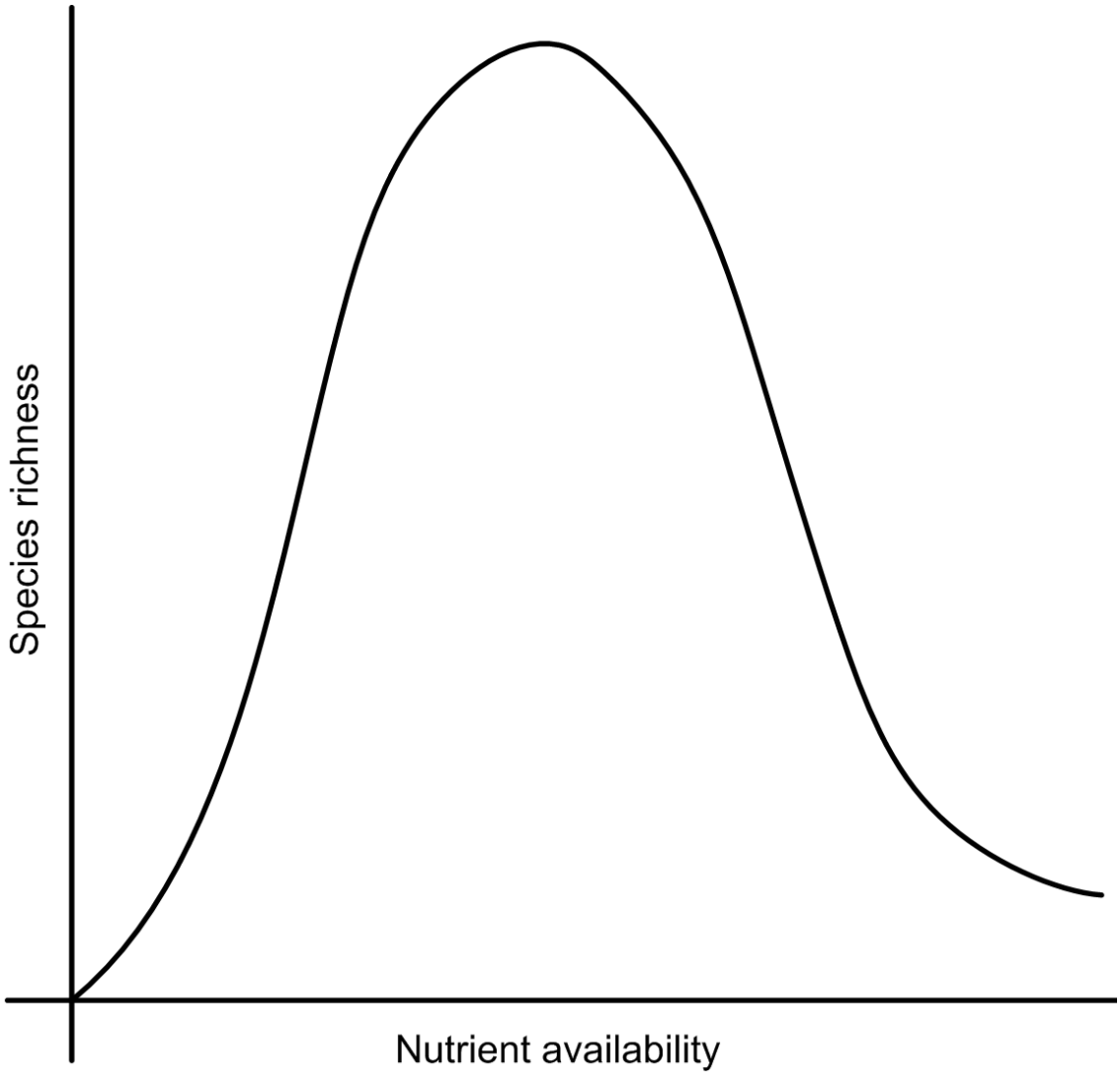

Figure 2.1: Relationship between nutrient availability and macrophyte species richness.

Alternative stable state theory, as put forward by Holling (1973) in the ecological context, holds that a system can have multiple equilibria in which it can exist. A perturbation of one or more environmental pressures is required for the system to move from one state to another position. Consider the existence of two possible states of stable equilibria in a lake: oligotrophic and eutrophic. An unstable mesotrophic equilibrium is assumed to exist between these two positions, as depicted in figure 2.2. In the case of an oligotrophic lake system becoming eutrophic, the perturbation can occur when nutrient levels increase. In order to recover from the eutrophic state, a greater perturbation of nutrient levels may be needed in order for the system to return to an oligotrophic state than was required for the system to enter a eutrophic state in the first place. Thus, the concentration of a particular nutrient of interest will need to be lower than it was initially, in order to return to this original state. With regard to figure 2.2, it is assumed the system is state A, i.e. in gravity well A.

Sufficient perturbation is needed in order for the ball to gain sufficient momentum to exit a gravity well. However, the effort to move the ball from gravity well A to gravity well B is less than to move it along the reverse of this path. In the same way with regard to a lake system, it requires a greater perturbation to move from a eutrophic system (B) to a oligotrophic system (A) than vice versa.

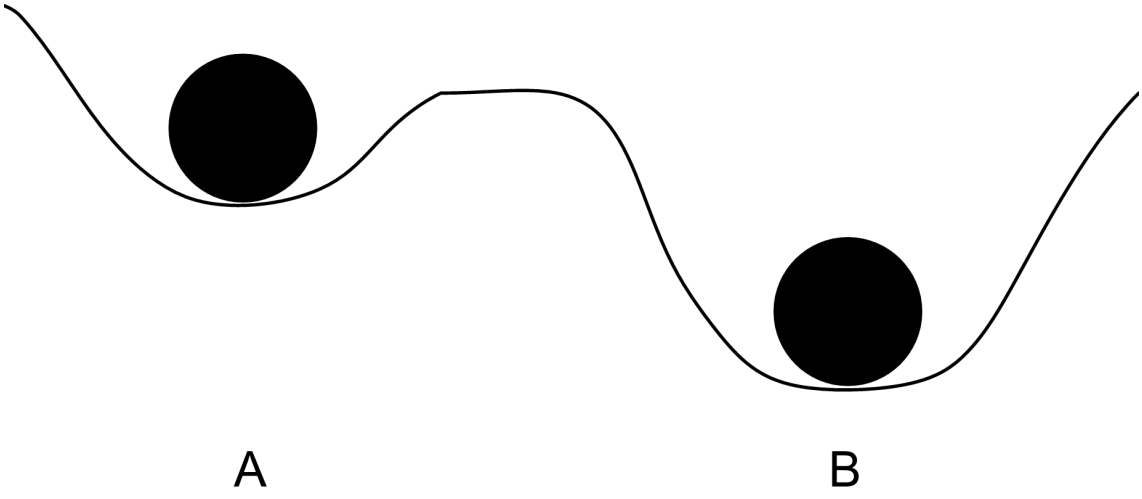

Figure 2.2: A graphical representation of the alternative stable state theory, with two gravity wells, A and B. Well A represents the oligotrophic status position; well B represents the eutrophic status.

2.1.2 Environmental pressures on macrophytes

Macrophytes are plants that grow in or near water; they are categorised as emerging, submerged or floating. In Britain they tend to grow initially in the spring of each year. Thus, conditions with regard to light and nutrient levels in the lake during this time are important. After this time if the plants have managed to grow to a sufficient length, they are above the turbid layers of the lake and therefore can obtain sufficient light levels higher in the water column later in the year. Thus it is conditions in the early part of the year that are important for the embedding of the submerged flora (Carvalho et al., 2012).

Due to shifts in nutrient and light levels, the habitat that the macrophyte community is able to colonise during this period is more easily inhabited by some species than others. Where a shift in the environmental pressures results in greater nutrient availability and decreased light levels, a less diverse community emerges, dominated by species that thrive in nutrient-rich conditions or those that cope better under lower light levels. The lake system could then be said to have moved from a stable oligotrophic state to a stable eutrophic state. It has been

suggested by Sand-Jensen and Søndergaard (1981) that the latter effect could be caused by greater turbidity in the water column or epiphytes on the surfaces of macrophyte species, which would increase shading and deplete nutrients at the host plant leaf surface.

A shift in phosphorus levels unbalances the system by way of benefiting some species more than others, due to certain submerged plant species being able to take advantage of the change in conditions and multiply faster in number. In a similar vein to the Ellenberg values outlined in chapter 1, Preston and Croft (1997) detail the preferred conditions of these species, by reference to the conditions under which they are most commonly found. For example, *Potamogeton praelongus* is generally found in mesotrophic conditions, in water deeper than 1 metre. *Zannichellia sp.* and *Potamogeton crispus* are more often found in shallow water of less than 1 metre in eutrophic lakes.

Phytoplankton tend to increase with nutrient levels. Given a short life cycle, the resultant increase in the amount of phytoplankton decomposition decreases oxygen levels in the water, which makes it more difficult for fish to live in the lake (Ludsin et al., 2001). Thus, a change in trophic status can affect other higher trophic levels above macrophytes. According to Søndergaard et al. (2013), macrophyte abundance is negatively affected by increased nutrient availability, which promotes both phytoplankton and epiphyte growth. This leads to increased turbidity and poorer water clarity.

The Maximum Growing Depth (MGD) of macrophytes in a lake is a standard measure used by the Water Framework Directive (2000) to understand lake health and is understood as a measure of the general lake condition. The MGD can be regarded as a resultant effect of other environmental factors that impinge upon the ability of the macrophyte community to colonise certain areas. The MGD of macrophytes in a certain year is therefore a surrogate measure of the general water conditions; it acts as a good indicator for water clarity and can be used to infer information about phytoplankton populations. High phosphorus concentration may lead to an increase in phytoplankton, and thus a decrease in water quality. A reduction in phosphorus concentrations in the lake leads to clearer water, as phytoplankton do not flourish under reduced nutrient levels. In turn a greater area of the lake is able to be colonised by macrophytes. An increased habitable area does not however directly indicate dominance or rarity of certain taxa that could be affected more directly by other drivers within the lake.

Nutrients, as well as being externally loaded into the lake are also leached from the underwater sediment. The roots of macrophytes contain the sediment and prevent it becoming disturbed, which prevents nutrients being leached from the lake bed. This prevents lake nutrient concentrations rising further. Thus, the lake bed stabilises and leaches less nutrients into the water column in areas that the macrophyte community colonise. When this occurs, the system could then be viewed as returning from a stable eutrophic state to a stable oligotrophic state, due to the change in lake nutrient levels and subsequent observed impact in the macrophyte community.

Søndergaard et al. (2010) showed a inverse relationship between MGD of macrophytes and total phosphorus (TP) concentration in a study comprising 300 lakes that exhibited differing macrophyte community responses. It was concluded that lakes that had lower TP concentrations had a greater MGD of macrophytes at the time of sampling. Thus, MGD can be a useful indicator of the water conditions at a specific lake.

Given this relationship between MGD and TP concentration observed over many lakes, the correlation of MGD with the spatial TP gradient is used to infer that the MGD in one particular lake will exhibit the same relationship with regard to the TP concentration over time. If the TP level rises then as described earlier, the MGD of the macrophytes will be expected to fall, unless another impacting driver were to alter the eutrophic effect.

In a subsequent analysis on a similar dataset covering about 750 lakes and over 900 lake years, Søndergaard et al. (2013) look at the correlation between MGD and a variety of covariates individually: Secchi depth, chlorophyll, total nitrogen and total phosphorus. The Secchi depth is the furthest depth at which a black and white disc lowered into the lake at a certain point is still visible. This gives a point measure of the water clarity and is thus indicative of the light level in the lake. Positive correlations are seen between the area colonised by the macrophytes and the explanatory covariates respectively, that lower nutrient inputs result in a greater area of the lake bed which can be colonised. MGD is observed to have strong positive correlation with Secchi depth than any of the other three environmental measures: the R^2 for the former covariate returned is 0.58 compared with 0.31, 0.31 and 0.24 for chlorophyll, total nitrogen and phosphorus respectively (Søndergaard et al., 2013). Given the number of lakes is very close to the number of lake years, and as in the analysis in Søndergaard et al. (2010), there is very little temporal information for individual lakes. There is also only single measurements of each variable for each lake year. However, the positive

correlation between MGD and Secchi depth indicates improved water clarity is correlated with an increase in the maximum depth colonised by macrophytes in the lake at that time. There is also very little information on species composition for the lakes of interest, so this response is not used in the analysis (Søndergaard et al., 2013).

Positive correlations between lake macrophyte species richness and maximum colonisation depth, mean colonisation depth and Secchi depth respectively are estimated by Vestergaard and Sand-Jensen (2000) in a study of over 70 lakes. Species richness of individual drag-rake samples with regard to environmental drivers and pressures were not assessed.

Other studies have looked at one particular lake over time: lake species richness in Lake Fure in Denmark was analysed by Sand-Jensen et al. (2008). Large variation in the phosphorus input to the lake has been observed since 1900; the lowest loads per year were observed at the beginning of the 20th century, which increased to values 30 times larger in 1970. A subsequent decline in annual phosphorus loads has been witnessed after this point. 17 surveys over the period of interest were used in the analysis. A multivariate ordination was conducted of the log relative abundance of the species sampled in order to show the change in the macrophyte community over the period of observation, from 1911 to 2005. Each survey conducted contained between about 150 and 270 samples. A partial Canonical Correspondence Analysis was conducted, to see how much variation in the community data could be explained by environmental covariates. Secchi-depth and nitrogen loading explained 41% and 31% of the variation in the response respectively. Given the number of samples in the surveys were different, surveys with more samples would have more chance of detecting rare species, which could affect the relative abundance estimations.

In summary, an increase in the TP load increases nutrient levels in the lake system, which leads to enhanced phytoplanton and epiphytic growth and thus lower light levels. The poorer light conditions result in a reduction in the area of the lake which is habitable by the macrophyte community. This is witnessed by a reduction in the MGD. As well, competitive macrophyte species take advantage of the nutrient-rich conditions, resulting in these species dominating the available habitat. This means there is a smaller chance of rare species being found in each survey and lower species richness across the lake. As the TP load decreases, the competitive species dominant less, due to the lower nutrient concentration accessible and so rarer species are able to increase in abundance. Epiphytic growth is reduced, resulting in an

increase in the area of the lake available for macrophyte growth. Thus, the probability of detecting rarer species increases and the observed species richness increases.

The discussed analyses of macrophyte communities in other lakes in the cited studies have been concerned with either the conditions at multiple lakes at single points in time or a single lake over an extended period. Attention is now turned to Loch Leven, the source of the data for this study, for which macrophyte data is available over an long period, making the lake suitable for trend analysis.

2.2 Loch Leven

Loch Leven, a lake of 13.3km^2 in area, is located in the East of Scotland in the Kingdom of Fife. The catchment area from which precipitation flows into the lake is approximately 142.5km^2. The surrounding land is mainly agricultural, but there are also urban and industrial areas close to the lake. A dam is located at the outflow point, to regulate the lake level and prevent flooding in farmland downstream. The maximum depth of the lake is 25.5m, and nearly half the lake area is shallower than 3m. Many species of wildfowl, plants and fish inhabit the lake system. Loch Leven has been a site of regular scientific measurement since the 1960s. Also, comprehensive surveys of the lake macrophyte population have been conducted there since as early as 1905.

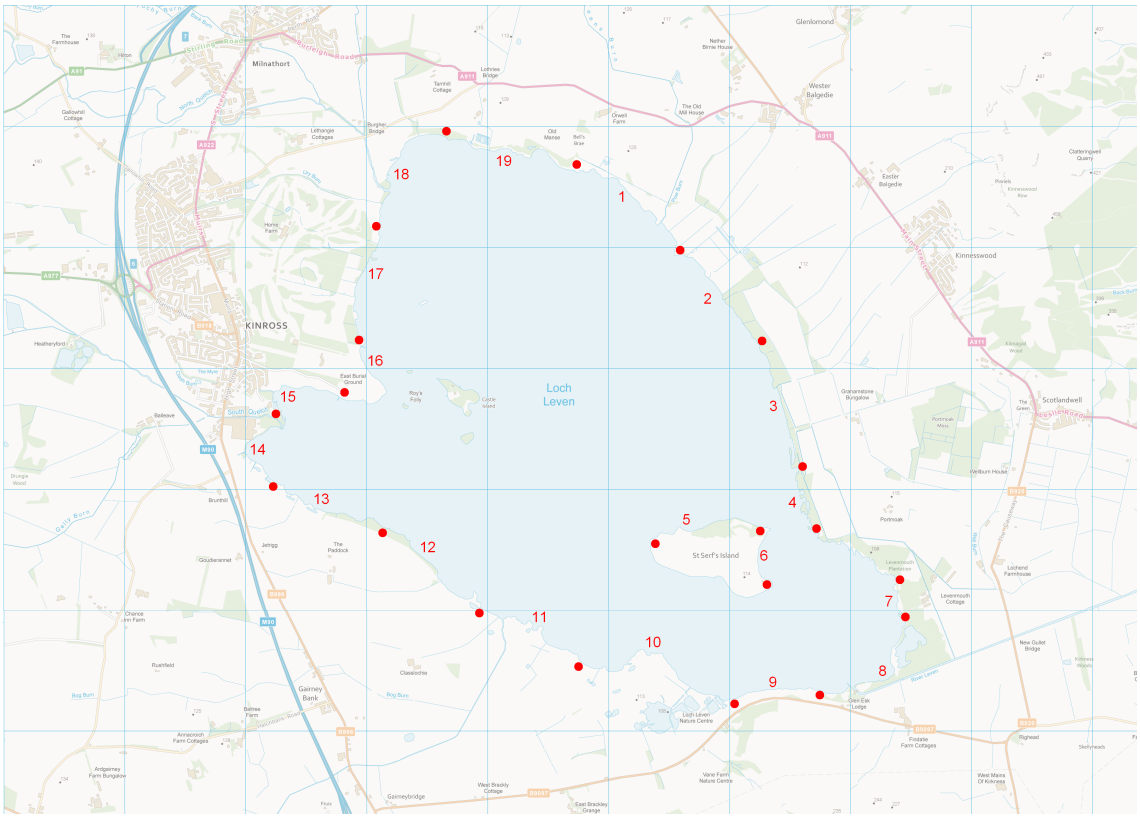

Figure 2.3: Map of Loch Leven, with sectors marked accordingly.

Over the last 100 years, the macrophyte community in Loch Leven has changed markedly. In 1905, West recorded the presence of 16 different taxon subsets in the lake; by 1966, the taxon richness had dropped to just 9 (Dudley et al., 2012). The reason for this shift in the number of taxa, is due to the fact that over the time period of these surveys, the lake underwent eutrophication, due initially to an increase in the annual loading of phosphorus into the system (May and Carvalho, 2010).

The source of a large amount of this phosphorus was a mill situated next to the lake, from which effluent entered into the lake during the period from the 1950s to the mid 1980s. A large phosphorus load comes via the inflow of tributary rivers and streams from agricultural run-off. River inflow contribution is extrapolated from samples made on each of the five main tributaries. Another prominent source is from geese; approximately 12,500 pink-footed geese spend the winter on the lake. May et al. (2012) estimate the contribution of phosphorus loading from the lake geese population using information on their diet, and thus the subsequent loading through excretion. Phosphorus also enters the water column via leaching from the lake bed, when sediment is stirred up by wave action into the water column.

The effluent from the mill, along with an increase in population and agricultural activity in the catchment led to the large shift in Total phosphorus (TP) loading. This change in TP annual loads into Loch Leven since 1905 has been studied by May et al. (2012) using the data displayed in figure 2.4, with a peak in loads to the lake during the late 1980s and subsequent reduction since then. The values in 1975 and 1986 are very different to each other; there is no definitive reason for the large variation in the 60s and 70s, although since about 70% of the annual external phosphorus input to the lake in this period is estimated to have come from a single industrial source, this may have resulted in large variation in the values, based on the changes in effluent entering the lake. In 1985 just under 60% of the phosphorus input was cited as from industry and sewage treatment; controls imposed on industry between 1985 and the mid 1990s are cited as the main reason for the reduction in TP input during this time (May et al., 2012). Changes in the chemical balance of the lake were analysed by Ferguson et al. (2008), who modelled the trends in SRP (Soluble Reactive Phosphorus) and $NO_3 - N$ in the lake over the last forty years. Nonparametric regression methods were used to fit the model over time, due to the nonlinear trend which is exhibited in the data.. The large number of data samples available allowed non-parametric splines to be fitted more easily to the data. There has been a recorded decrease in the concentration of SRP since the mid-1970s, but not in $NO_3 - N$. Apart from months and years, no other covariate data is used in the models to explain the variability in the responses. The data are also not used as explanatory covariates in modelling potential dependent variables. However, given their importance for macrophytes and phytoplankton, both phosphorus and nitrogen are nutrients which could act as drivers in the eutrophication process.

As a result of the change in TP annual loads over the over the past century, the macrophyte population has changed composition and colonisation areas. The macrophyte MGD as a response to TP loading was studied by May and Carvalho (2010), showing a negative correlation in the relationship; as the TP load has decreased, an increase in the MGD has been observed. With an R^2 value of 0.64, the estimated load of TP into the lake in a specific year does not show a very strong correlation with MGD, but it was indicative of a causal effect of the TP over time, which has an indirect effect on the colonising ability of macrophyte species each year. This relationship is used to infer that the change in phosphorus loads to the lake were responsible for the eutrophic conditions. There was not however, as strong a relationship between TP concentration in the lake and the MGD. This was thought to be because a reduction in TP load levels is not immediately reflected in an increase in MGD. However the MGD of the macrophytes at any point in time is a lagged response to the 'light history' of the lake over the past few years before the MGD measurement is taken (May and Carvalho, 2010).

Lower light levels make it more difficult for macrophytes to inhabit an area of the lake bed, since light is an integral part of the photosynthesis process. A graph of the recorded maximum growing depths values of macrophytes in Loch Leven is shown in figure 2.5. Only those values corresponding with comprehensive macrophyte surveys are depicted. The earliest survey in 1905 recorded macrophytes at a depth of just under 5 metres. The next survey was over 60 years later, in 1966, where the MGD was 2 metres; the subsequent surveys up to and including 1993 returned measurements of MGD around this value.There then followed a increase in the MGD in 1999 and again 2008; the latter of which recorded macrophytes at a a depth of 4.5m.

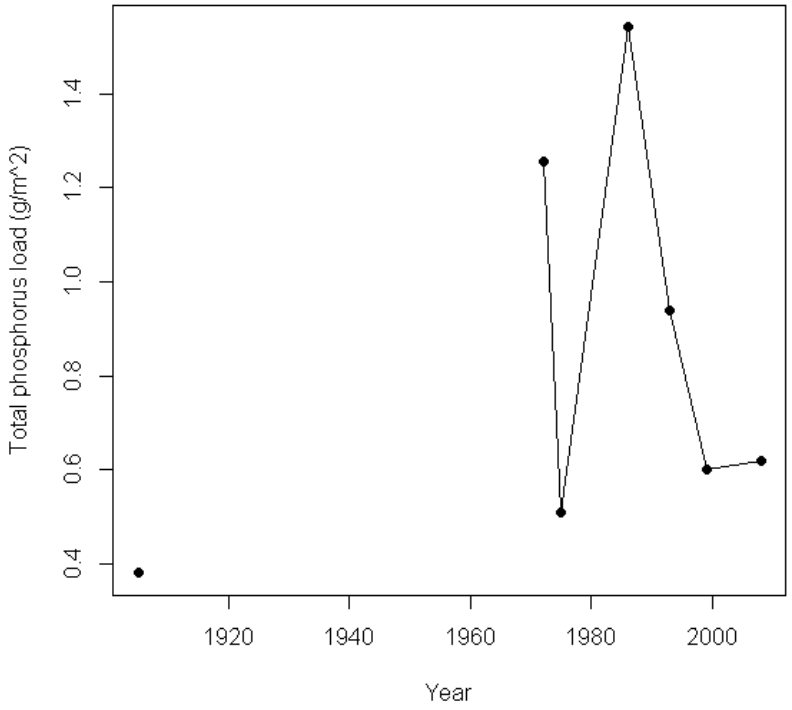

Figure 2.4: Estimated TP load in Loch Leven, by survey. The 1905 value was estimated using palaeolimnological samples. Data are a subset of those in figure 3 in May *et al.* (2012) May et al. (2012).

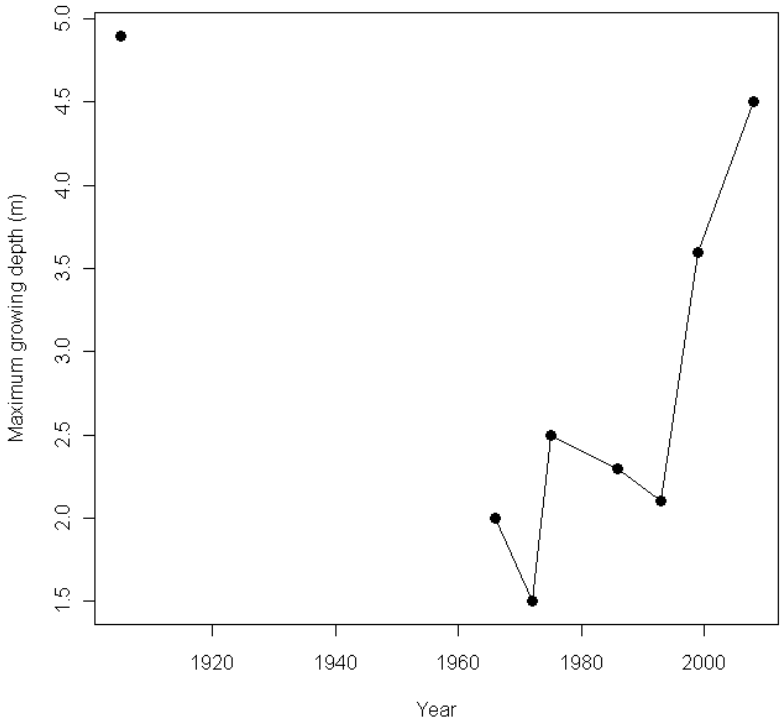

Figure 2.5: Maximum growing depth of macrophytes recorded in each survey.

Two main effects are posited by May and Carvalho (2010) as being responsible for the change in macrophyte colonisation area over time: phytoplankton and epiphytes. Firstly, under increased phosphorus loading, phytoplankton are able to flourish and grow in number quickly each year, due to the relatively high prevalence of nutrients, resulting in lower levels of water transparency for the macrophytes, which are then unable to colonise the lake bed below. Another possible effect is that of epiphytes, plants which can grow upon other macrophytes, increasing shading on the macrophytes themselves. Both these effects would lead to deeper sections of the lake not being inhabited by the macrophyte community. With macrophyte roots not embedded in certain parts of the lake bed, the sediment would be disturbed more easily into the water column by wave action. This would lead in turn to more nutrients being leached from the lake bed, increasing the nutrient concentrations in the lake still further.

May and Carvalho (2010) state the general belief that light levels and water turbidity over the period of time prior to survey are probably the most important drivers of MGD. Thus, changes in MGD are considered to be indicative of the recent history of the state of the lake. In order for the water quality in Loch Leven to achieve 'good' statuses according to the Water Framework Directive targets, the Loch Leven Catchment Management Project (1999)

set several targets. One of these targets was for the MGD of macrophytes to reach a level of 4.5 metres.

Dudley et al. (2012) assessed the changes in the macrophyte community since 1905, using all known comprehensive surveys of the lake system. Several metrics, such as presence-absence and taxon richness were used to infer recent recovery of the macrophyte community, both across the lake as a whole and within separate regions of the lake. However, explanatory covariates such as TP loads were not used in the analyses. The untested hypothesis is that the biodiversity of the macrophyte community is dependent upon the lake condition. Statistical inference is needed therefore, to link change in possible drivers and surrogate water quality measures with recorded shifts in the macrophyte community.

2.2.1 Aim

In light of the aforementioned study by Sand-Jensen et al. (2008) linking the 'states' of water clarity and MGD with the 'impact' of change in macrophyte species richness, there is a need to analyse the data available for Loch Leven on the issue, in order to see if similar relationships can be observed between environmental covariates and the macrophyte community response. It is also important to take the TP load 'pressure' into account in the modelling process, given its highlighted importance as being negatively correlated with MGD. This study will look at taxon richness change at the lake level since 1905 and subsequently within distinct lake areas since 1986. Charophytes and chlorophyta are included as macrophytes in the response as well, as although they are not strictly macrophytes, they inhabit the same areas of the lake and distribute themselves in a similar way.

The macrophyte community will be assessed with regard to how the community has changed over the period of eutrophication. As stated previously, in Loch Leven there is a clearly understood relationship between the TP loading into the lake system and the MGD. What has not been analysed in such detail is the diversity of the macrophyte community. Thus, it is important to understand the relationship at this location between the environmental drivers and pressures and the biodiversity response. This will be performed with regard to environmental covariates: the total phosphorus (TP) lake loading estimates and maximum growth depth (MGD) of the macrophytes as a proxy measure of lake condition. The difference in macrophyte response between sectors across the lake will also be assessed and also the responses compared at the whole lake and fine-scale, sample levels.

In the next section I will discuss the sampling methods that have been carried out in comprehensive surveys since 1905 and the modelling approaches that will be used in light of these methods.

2.2.2 Surveys

Table 2.1 gives the year, sampling method, sample length and number of samples for each survey used in the analysis. The first comprehensive survey of the macrophyte community in Loch Leven was conducted by West in 1905 (Dudley et al., 2012). This survey is thought to have been comprehensive in terms of the geographic extent of the lake, as it was conducted alongside a bathymetric survey of the lake. Only a taxon presence-absence list was made, with no record of the abundances available. All surveys used a form of drag-rake to extract samples of macrophytes from the lake bed. Samples are known to have been taken in line transects from 1966 onwards. In 1966 and 1972, Pollard conducted surveys of the lake recording the abundance of each species in each transect, as well as the survey sample size. Surveys were conducted in 1975 and 1986 by Bailey-Watts and Robson respectively. Transects were made along lines perpendicular to the general line of the lake edge; they start at the land, and samples are made at regular intervals into deeper water. Dudley et al. (2012) state that transects in all surveys were determined prior to being sampled, although the same transects were not necessarily repeated by subsequent surveys; samples between 1966 and 1986 were conducted from a moving boat with a drag-rake (a double-headed metal rake with long prongs) pulled behind the craft (Dudley et al., 2012). Only since 1986 has the presence of each taxon found in each sample been recorded. In each sample this is recorded as binary data: there is no record of abundance of each species. In 1986 the distance that the drag-rake was pulled under the water for each sample was between 5 and 129m in length. Since 1993, this distance has been 2 metres in length. Some samples in the 2008 survey were made using a bathyscope (an underwater viewing device) to minimise disturbance.

The lake is divided up into 19 defined sectors. Every sample from 1986 onwards can be attributed to a specific sector of the lake, displayed in figure 2.3. The position of transects within each sector or the position of individual samples is not known in further detail for all surveys. All sectors are defined according to the section of the lake edge to which they are adjacent, with the exception of two sectors, which are defined by their adjacent position to St. Serf's Island, in the south-east corner of the lake. This means, from 1986, the presence-absence of each taxon found in each individual drag-rake sample was recorded. For the

surveys before 1986, only the presence-absence of taxa for the whole lake is used in this analysis.

Year	Surveyor(s)	Sampling method	Sample length	No. samples	Sector noted
1905	West	-	-	-	No
1966	Pollard	Drag-rake, moving boat	-	-	No
1972	Pollard	Drag-rake, moving boat	-	-	No
1975	Bailey-Watts	Drag-rake, moving boat	-	-	No
1986	Robson	Drag-rake, moving boat	5-129m	165	Yes
1993	Murphy and Milligan	Drag-rake	2m	150	Yes
1999	Griffin and Milligan	Drag-rake	2m	170	Yes
2008	CEH internal study	Drag-rake, bathyscope	2m	256	Yes

Table 2.1: The comprehensive macrophyte surveys known to have been conducted in Loch Leven. The year, lead surveyor, sampling method, sample length in metres and number of samples are displayed, along with whether the lake sector was recorded in which each sample was made. The '-' symbol denotes an unknown value or method. There is a large time gap between the first two surveys, but since 1966 the largest period between surveys was 11 years between 1975 and 1986.

Only half of the surveys in this dataset are available with data at the drag-rake sample level delineated by Sector. The positions of these samples is not always known precisely and there are not always the same number of samples in each sector or survey. For the surveys where Sector is known for each drag-rake sample, the variability between and within Years and within Year, between and within Sectors will be analysed, in order to assess how much variation is present in the data at these levels. For the same subset of data, the correlation between model residual values across the lake as a whole will also be assessed, in order to see if there is an underlying spatial pattern.

2.2.3 Macrophyte community

The total taxon richness of the macrophyte community recorded in each of the aforementioned surveys is displayed in figure 2.6 and table 2.4. The presence of different species over

time is remarkably varied (Table 2.2). *Potamogeton gramineus* and *Potamogeton lucens* have not been recorded since 1905. Also, using historical and palaeolimnological records, (Salgado et al., 2010) note that several species were recorded only prior to 1905, such as *Isoetes lacustris* and *Subularia aquatica* and have not been recorded since 1821 and 1836 respectively. It is possible that these species have disappeared from the lake, however absence of a species from the lake cannot be inferred from its lack of presence in survey data. The surveys conducted in the 19th century are not known to be comprehensive in coverage or sampling effort, so they have not been used in this analysis.

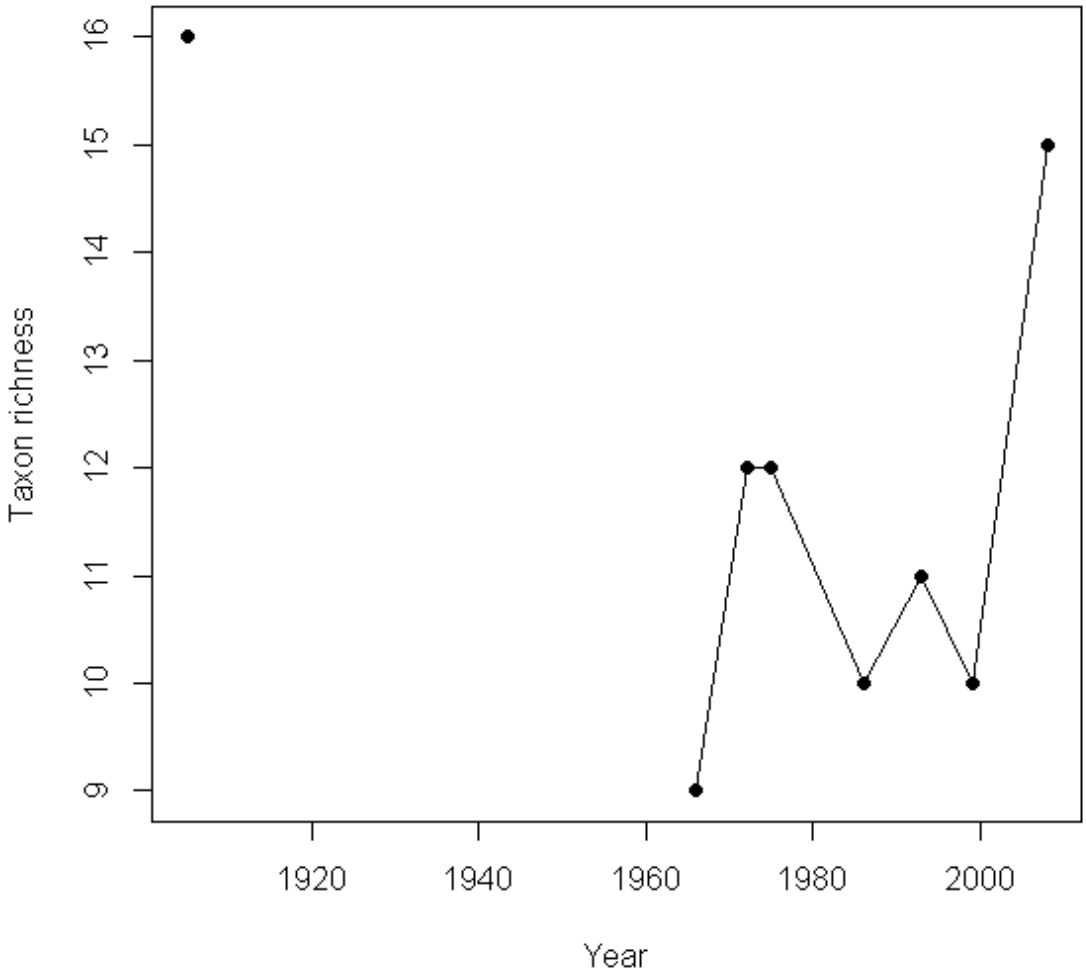

Figure 2.6: Taxon richness of macrophytes in Loch Leven, by survey.

Group	Group taxa	1905	1966	1972	1975	1986	1993	1999	2008
1	Callitriche hermaphroditica	*		*	*	*	*	*	*
2	Ceratophyllum demersum		*						
3	Chara sp.	*	*	*	*	*	*	*	*
4	Chlorophyta					*	*	*	*
5	Eleocharis acicularis	*			*		*	*	*
6	Elodea canadensis	*	*	*	*	*	*	*	*
7	Fontinalis sp.			*		*			
8	Juncus bulbosus		*						
9	Littorella uniflora	*		*	*	*	*	*	*
10	Myriophyllum sp.	*	*	*					*
11	Nitella sp. Tollypella sp.	*	*	*	*				*
12	Persicaria amphibia								*
13	Potamogeton crispus		*	*	*	*	*		
14	Pot. gramineus	*							
15	Pot. lucens	*							
16	Pot. obtusifolius	*	*	*					
17	Pot. perfoliatus	*		*	*	*	*	*	*
18	Pot. praelongus	*							*
19	Pot. x zizii	*							
20	Pot. filiformis Pot. pectinatus	*	*	*	*	*	*	*	*
21	Pot. berchtoldii Pot. pusillus	*			*		*	*	*
22	Ranunculus sp.	*							*
23	Zannichellia palustris			*	*	*	*	*	*

Table 2.2: All taxa recorded in Loch Leven and their presence-absence in each survey, as denoted by an asterisk. Charophytes and chlorophyta are included as part of the macrophyte community; they have been denoted by their respective singular groups.

Sample 1	Sample 2
Callitriche hermaphroditica	Nitella/Tollypella
Potamogeton perfoliatus	Ranunculus sp.
Potamogeton berchtoldii/pusillus	Potamogeton filiformis/pectinatus
Ranunculus sp.	

Table 2.3: An example of two sample records from the 2008 survey. No distinction is made in the records between the genera *Nitella sp.* and *Tollypella sp.*.

Diversity indices

As discussed in section 1.3, many diversity indices aid the analysis of biological data, by calculating a univariate value from information on the evenness and heterogeneity of species' abundances. The intention of such an index is to depict the relative abundances of each taxon in a suitable single figure. Table 2.3 gives examples of two samples from the 2008 survey; the taxon richness of the first sample is 4 and the taxon richness of the second sample is 3. In this study indices based on the evenness of the samples will not be used for transects because as previously stated, only presence is recorded within each sample and the number of samples in each transect and number of transects in each sector of the lake is not uniform. Therefore, it could potentially be biased to compare indices of transects or sectors which are based on different numbers of samples, since the sampling effort would differ. The taxon richness of each sample or the lake as a whole will be used as the model response, which is an index based solely on heterogeneity. Before 1986, records did not reveal how many samples were in each transect.

Species presence-absence for the whole lake is chosen as the initial response, since, although the sampling intensity is different, the species recorded are known to be there; in older surveys, it may be argued that they were relatively intensively sampled, due to the very long sampling distances, over which a drag-rake was pulled through the water, as stated previously. The other measure to be used is the number of species found in each sample. This is always at least 1, presumably because samples were only collected where species were present; beyond a certain distance macrophytes cannot grow because the water is too deep, as specified by the maximum growing depth measurement (MGD).

For the post-1975 surveys only, since presence of each taxon within each sample is recorded, abundance within each drag-rake sample is unknown. Earlier survey records do not mention

specific sample presence-absence. Taxon (instead of species) richness is used in the analyses, due to the difficulty in differentiating between certain species of the genus *Potamogeton*, for instance. Also, some species have been combined into by genus, due to data throughout time not being immediately comparable at the species level.

Year	MGD (m)	TP load (g m^{-2})	Taxon richness
1905	4.9	0.380	16
1966	2.0	*	9
1972	1.5	1.255	12
1975	2.5	0.508	12
1986	2.3	1.541	10
1993	2.1	0.940	11
1999	3.6	0.602	10
2008	4.5	0.619	15

Table 2.4: Maximum Growing Depth (MGD) of macrophytes, TP load and taxon richness, by year. The '*' symbol indicates the absence of an estimated covariate value for TP load in 1966.

Having discussed the survey data available, an initia multivariate analysis of all comprehensive surveys will be conducted, followed by regression modelling of the taxon richness response.

2.3 Analysis

2.3.1 Assessing macrophyte community change

Taking the presence-absence data of each taxon, a multivariate analysis technique was used in the analysis. Classical Multi-Dimensional Scaling (MDS) aims to represent the composition of taxon presence-absence by survey, using fewer dimensions than the dimensionality of the data (Digby and Kempton, 1987). Whereas the matrix of the presence of all taxa would require 18 dimensions to view all the information contained within it, since there are 18 different taxa in the analysis. The variability between the surveys in so many dimensions cannot easily be represented in a single graph.

Instead, Classical MDS represents the difference between the surveys, along the two axes which depict the greatest variability. This affords a simple representation of the data, as a part of a preliminary analysis. If there are r different taxon groups, the distance between two surveys, i and j is the Euclidean measurement:

$$d_{ij} = \sqrt{\sum_{k=1}^{r} \left(z_{ik} - z_{jk}\right)^2}, \tag{2.1}$$

where

$$z_{ik} = \begin{cases} 1 & \text{if taxon } k \text{ is recorded in survey } i \\ 0 & \text{otherwise} \end{cases} \tag{2.2}$$

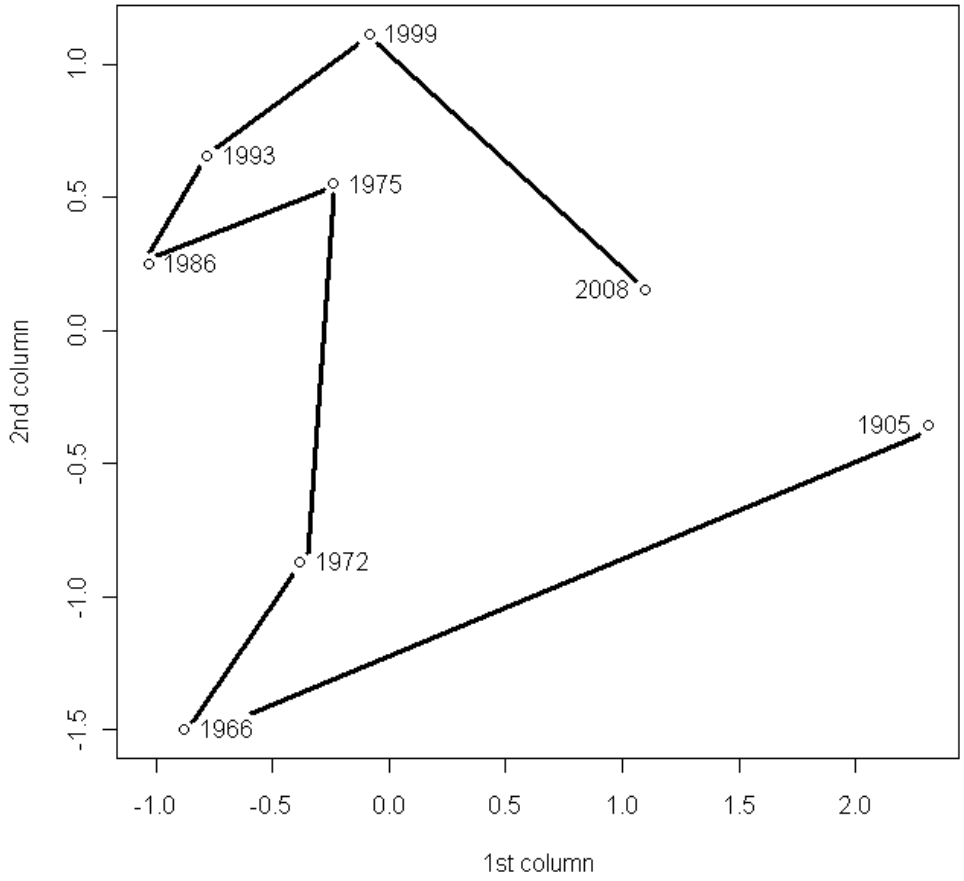

Figure 2.7: Multidimensional scaling of the presence-absence data from the Loch Leven comprehensive surveys. It uses Euclidean distances in the calculation, as outlined in equation 2.1. Figure adapted from figure 4 in Dudley *et al.* (2012) Dudley et al. (2012).

Figure 2.7 depicts a multidimensional scaling of presence-absence data of the macrophyte species. The first two axes represents approximately 70% of the variation in the data; 45% and 25% for the first and second axes respectively. Along the x-axis, showing the greater variability, there appears to be an emergent pattern of the shift in community dynamic from right to left on the graph from 1905 to 1966, with a reversal in trend for recent surveys, from 1986 to 2008. The y-axis represents the movement from 1966 to 1999. As stated, these axes do not depict all the variability in the data; 30% of this variability cannot be visualised using this result. Additionally, this is only a presence-absence model, with no covariates included in the modelling of the data.

It should be stated that the result generated by the multidimensional scaling is only a representation of the data, depicting the relation of the macrophyte community in different surveys to each other and not an understanding of how the macrophyte community is affected by environmental drivers, or indeed how significant the effects are. Given these limitations, a explanatory model structure inclusive of covariates is desired, in order to assess the driver impacts. Inference as to the effect of the environment on the macrophyte community can be made in a linear model: taxon richness will be used as the response variable in the following models.

2.3.2 Introducing explanatory covariates

TP load estimates (Figure 2.4, Table 2.4) are used as a covariate for each respective survey year. Phosphorus loading into the lake is understood to be a 'pressure' in the **DPSIR** framework. The TP load value for 1905 is estimated from palaeolimnological records, and in more recent surveys, the method outlined in a study by May et al. (2012) is used. When the estimate TP load is greater, the lake TP concentration in this period is inferred be higher. This leads to eutrophication, where a few taxa may tend to dominate the available area in which macrophytes are able to exist. These taxa which prefer high-nutrient conditions prevent other taxa from being as widespread. Thus, at times when the estimate TP load is greater, the lake TP concentration will be higher, and the taxon richness within each drag-rake sample, but also across the lake as a total will be lower. As noted earlier, the nutrient conditions in the spring of the year are important for the embedding of the macrophytes. However, TP loading data are only available for the whole of each survey year of interest. Thus the annual TP load is considered a surrogate measure of the TP load in the early part of the year. Year itself is included as a covariate to look at the trend over time, in order to see if the taxon richness

in individual drag-rake samples and across the lake as a whole is occurring not as a result of known effects within the lake, but a general intra-community process over the period of analysis.

The MGD covariate is considered a surrogate measure of the area of the lake colonised by macrophytes. A lower value of MGD is indicative of greater TP loads in the recent preceding period, which has led to higher lake TP concentration. This in turn leads to eutrophic conditions. Thus, when MGD is lower, a similar response is expected in the macrophyte population, and would be witnessed in individual drag-rake samples and in the total sample taxon richness.

The trend in different areas of the lake could vary. Therefore sector is included as a factorial covariate to look at the difference between these sectors. Secchi-depth could be included, as a surrogate measure of water turbidity. Contemporaneous Secchi-depth measures were unavailable, however this measurement is linked to the MGD of macrophytes as they are both different surrogate measures of water clarity. Figure 2.5 shows the recorded macrophyte MGD in each survey.

2.3.3 Modelling lake taxon richness

The number of comprehensive surveys available is very limited, and the number of suitable covariates is also small. Given the small number of response values, a relatively simple model will be fitted. Therefore, the initial model set up in this scenario is a linear model, structured as follows:

$$y_i = \mathbf{X}_i\beta + \varepsilon_i,\ i = 1,\ldots,n \tag{2.3}$$

where y_i is the ith response, $\mathbf{X}_i$ is the ith row of the covariate matrix, β is the respective vector of parameters, $\varepsilon_i \sim N\left(0,\sigma_\varepsilon^2\right)$ is the residual error with variance σ_ε^2 and n is the number of response data.

As previously discussed, data on the abundance of each taxon are not available for the 1905 survey, only a taxon list of everything found in the lake. Thus, in order to include these data in the model, the response used in the model will be the lake taxon richness (Figure 2.6). There was a marked decrease in taxon richness between the maximum value observed in 1905, and the much lower values from 1966 onwards. However, a recovery is witnessed in the latter years. The explanatory covariates in the model to be tested are TP load to the lake in grams m^{-2} in the year of survey and maximum growing depth (MGD) of the macrophytes in each survey, as well as the year of survey. All three covariates are treated as linear. The model is fitted using the likelihood of the parameter coefficient vector, β. Given the response vector $\mathbf{y}$, this is performed by maximising the function $L(\beta)$ where:

$$L(\beta) = \prod f_{\theta_i}(y_i), \tag{2.4}$$

where $f_{\theta_i}(y_i)$ indicates the Normal distribution with identity parameter θ in this case. Backward selection was used, with the criteria of AIC value and the significance of the covariates employed in the choice of model. As can be seen, MGD was the sole significant covariate (Table 2.5). The deviance explained is calculated relative to a null model with a mean term fitted as the sole fixed effect.

For every extra metre of lake depth which is colonised the taxon richness increases by an estimate of 1.46 (table 2.6). The estimate for the MGD coefficient is 1.46, with a standard error of 0.54; the adjusted R-squared value is 0.48. Given the poor structure of data, the model has limited ability to explain the variation in the response and there is little information on any potential violation of the model assumptions (Figure 2.8). Due to the lack of data for fitting this model, the ability to assess the goodness-of-fit and the model assumptions are curtailed More data points would be needed to test that the assumptions have not been violated. Given the small number of response values, it would have been difficult to fit a model with more than one covariate. However just under half of the variability is unexplained by the model. Although the data are very sparse, the result is informative for comparison with further analyses when looking at taxon richness over time at the drag-rake sample level. The four most recent surveys had comparably similar methods of recording the data and allow an individual sample taxon richness model to be fitted using only the data from these surveys.

Model	Covariates	AIC	Dev. expl.
1	TP*MGD+Year	34.0	71.6%
2	TP+MGD+Year	33.8	63.3%
3	MGD+Year	36.6	60.9%
4	**MGD**	**35.7**	**55.3%**

Table 2.5: Linear model results from taxon richness by survey model; model 4 is the chosen model.

Covariate	Coef. est.	P-value
Intercept	7.5774	<0.01
MGD	1.4692	0.03

Table 2.6: Linear model results from model 4 in table 2.5. The final selected model returns the maximum depth of macrophyte growth as sole explanatory covariate in the model (Table 2.5).

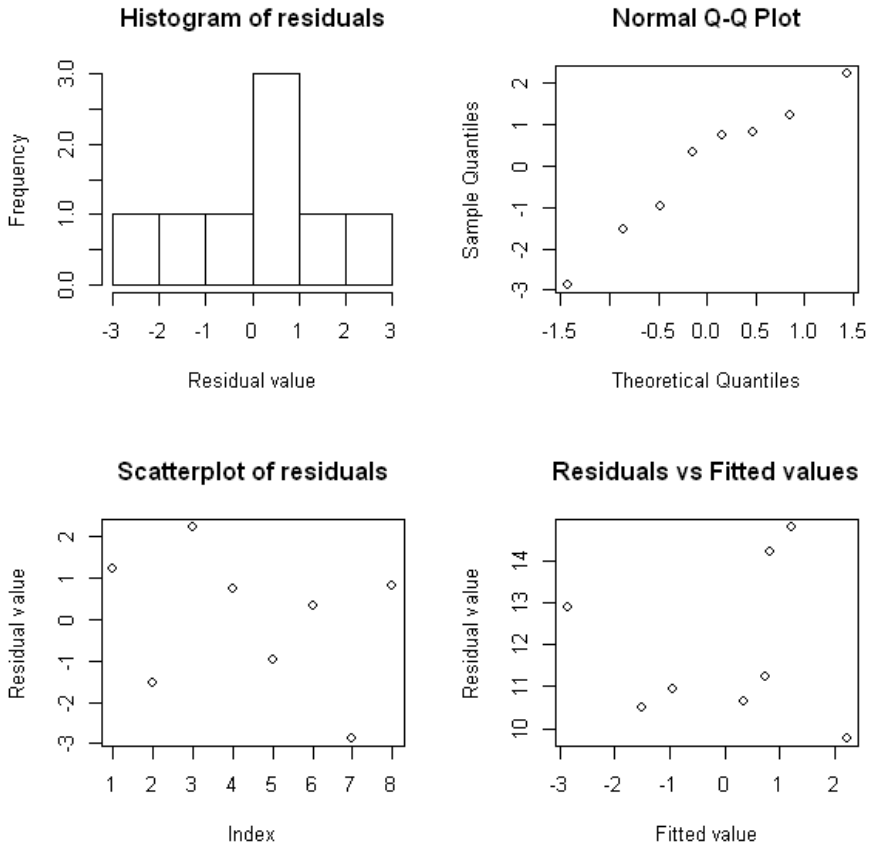

Figure 2.8: Diagnostic plots of lake taxon richness linear model.

2.3.4 Modelling sample taxon richness

Having fitted an initial model to the lake taxon richness, focus is now turned to sample taxon richness across the lake. Not all the surveys include information on the Sector in which each drag-rake sample was taken. The only surveys to record taxon richness in each sample are the four most recent surveys. Thus, the response of the macrophyte community to environmental covariates can only be modelled at this scale over a period of about 20 years, rather than 100, as in the previous model in table 2.6. Histograms of the taxon richness per sample are depicted in figure 2.9.

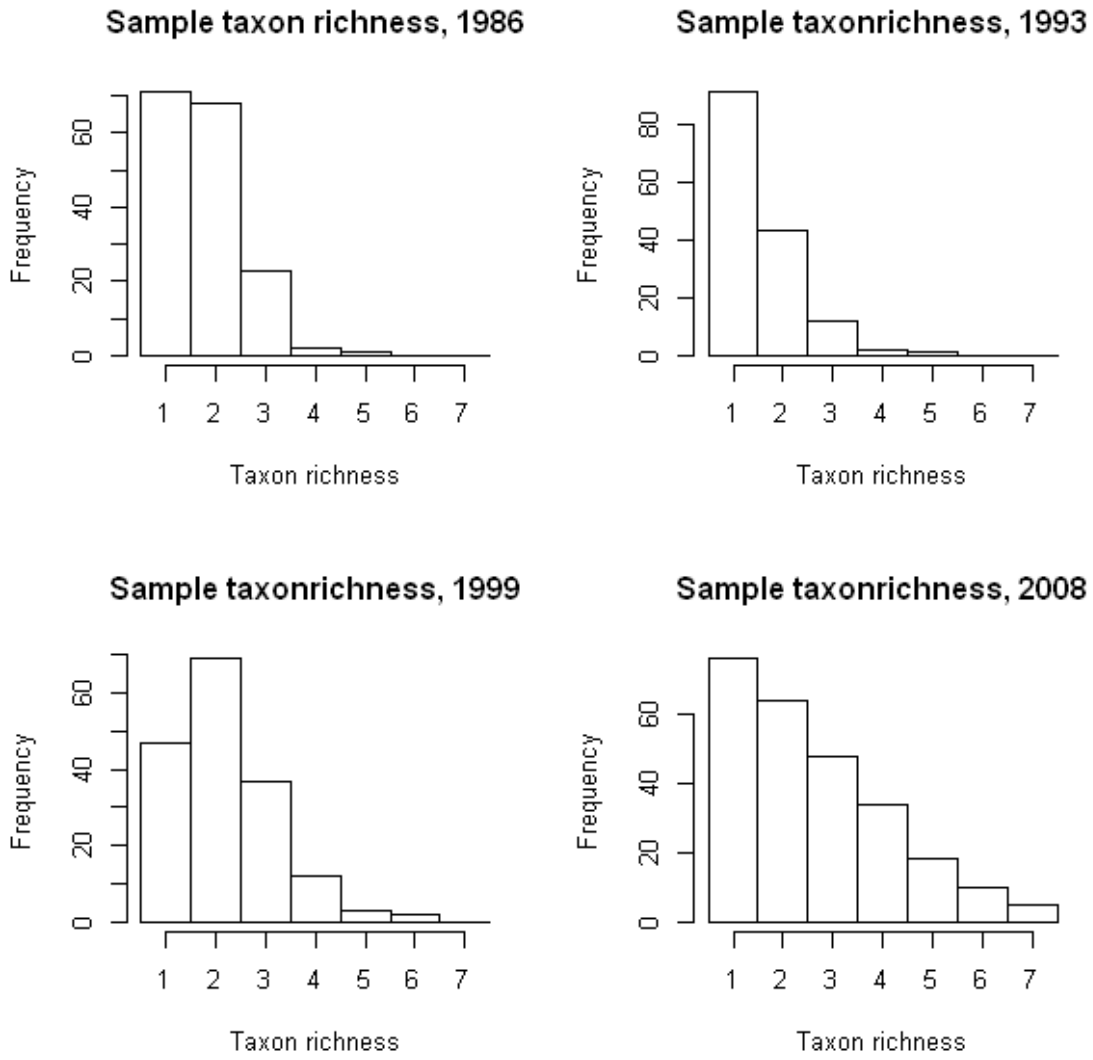

Figure 2.9: Histograms of the frequency of taxon richness per sample in each of the four latest lake surveys.

In an extension to the linear model in equation 2.3, the response data here are fitted using a Poisson distribution model. A negative binomial distribution was tested but deemed to be poorer fitting than the Poisson. The Generalised Linear Model (GLM) setup allows the response variable, $g(y_i) \sim \text{Pois}(\lambda)$. The model is:

$$g(\mu_i) = \mathbf{X}_i\beta \tag{2.5}$$

where $\mathbf{X}_i$ is the ith row of the covariate matrix and β is the parameter vector. The structure allows the use of a link function, $g(\mu)$, where $\mu \equiv E(y_i)$. By way of the function, g, the GLM extends the linear model by allowing the fitting of non-normally distributed response data. The Poisson model is suited to this dataset as it is intended for use with count data. In the following GLM and GLMM structures, g will be the logarithmic link function. The model is fitted as per equation 2.4, where $f_{\theta_i}(y_i)$ indicates the Poisson distribution.

As before, the TP load estimates, MGD of macrophytes and Sector are used as explanatory covariates; Sector is fitted as a factor. The model process is conducted again using backward selection, fitted using Maximum Likelihood.

Model No.	Covariates	AICc	% Dev. expl.
1	MGD*TP*Sector	2344.4	33.6
2	MGD*TP + TP*Sector + MGD*Sector	2322.0	30.7
3	MGD*TP + MGD* Sector + TP	2293.5	28.5
4	MGD* Sector + TP	2293.5	28.5
5	MGD + Sector + TP	2287.1	24.0
6	**MGD + Sector**	**2276.3**	**23.4**
7	MGD	2283.7	14.1
8	Sector	2286.8	15.2

Table 2.7: The generalised linear model results from taxon richness by sample model with associated AICc values; model 6 is the chosen model.

The results of the GLM are shown in table 2.8. MGD and Sector are the included covariates. The coefficient of MGD is 0.17, indicating that for every metre deeper the macrophyte population is observed, the mean sample taxon richness increases by about a sixth. Of the Sector coefficients, six of the nineteen sector coefficients are significant at the 5% level. These are Sectors 6, 7 , 11, 12, 15 and 17, which have positive coefficients between 0.25 and 0.44, indicating a higher mean sample taxon richness. All other sector coefficient are not significant.

Covariate	Coef. est.	Std. Error	P-value
MGD	0.17	0.03	<0.01
Sector 1	0.04	0.22	0.86
Sector 2	0.03	0.14	0.82
Sector 3	-0.121	0.12	0.32
Sector 4	0.119	0.20	0.55
Sector 5	-0.15	0.16	0.38
Sector 6	0.25	0.11	0.02
Sector 7	0.44	0.16	<0.01
Sector 8	0.13	0.15	0.38
Sector 9	-0.06	0.18	0.74
Sector 10	3.65×10^{-3}	0.19	0.98
Sector 11	0.42	0.14	<0.01
Sector 12	0.35	0.16	0.03
Sector 13	0.13	0.14	0.37
Sector 14	0.25	0.14	0.06
Sector 15	0.31	0.13	0.02
Sector 16	0.01	0.15	0.95
Sector 17	0.34	0.15	0.03
Sector 18	0.32	0.20	0.12
Sector 19	0.14	0.19	0.45

Dispersion parameter	0.53

Table 2.8: Table of the parameters from the chosen GLM, model 6 in table 2.7. The models tested with fitted with an intercept term, but given the inclusion of Sector in the model, the intercept term has been removed, so that the Sector coefficients are easier to interpret and are not estimated relative to the first sector.

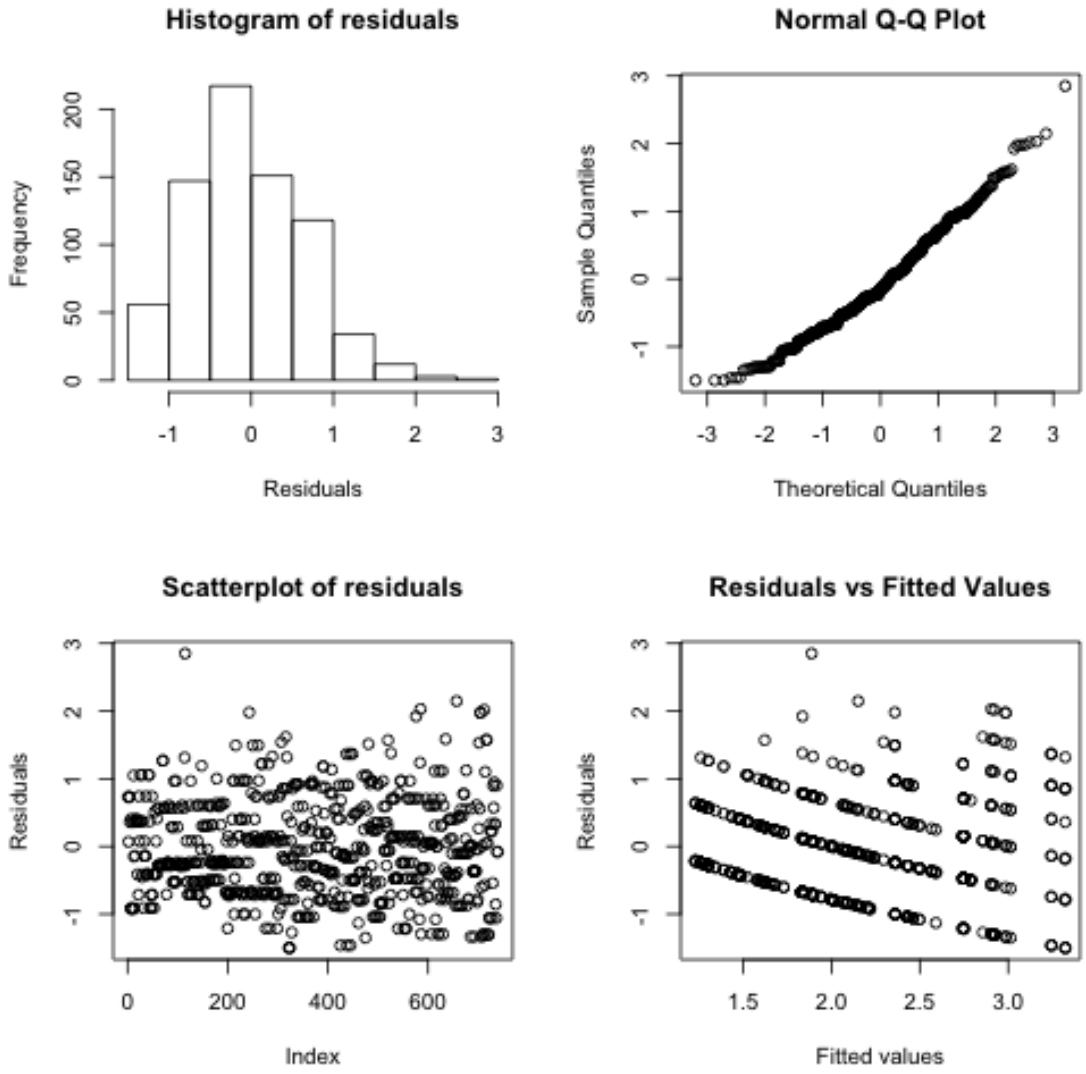

Figure 2.10: Diagnostic plots of the sample taxon richness generalised linear model (GLM).

The residual plots depicted in figure 2.10 show a slight sign of deviation from the expected distribution in the upper two plots. Given there is only one covariate in the final model, there is little information in the lower right plot as to the presence of heteroscedasticity in the residuals. A null model with a mean term fitted is used for comparison, in order to assess how much of the deviance has been explained by the covariates in the final model. The deviance explained in the final model is shown in table 2.7 is calculated in reference to this model: approximately one quarter is explained by the chosen model in table 2.7. This indicates there is still a considerable proportion of variability in the response data which cannot be explained by the model covariates.

2.3.5 Introducing random effects

In furthering the analysis of sample taxon richness, the variability between years and between sectors within years is desired to be estimated. These estimates are calculated using a Generalised Linear Mixed Model (GLMM). The same covariates are used as fitted effects, as in the GLM. IN addition, Year is included as a linear fixed effect. Given that that there are multiple samples within each year, there are pseudoreplicated responses within each survey year. To account for the pseudoreplication, Year is included also as a random effect. As well as being fitted as a fixed effect, Sector is nested within Year as a random effect in order to estimate the variability between sectors within years and to assess the difference this has on the chosen fixed effects. Due to sector 18 being sampled in only one of the four surveys, this sector is removed from the model. The GLMM allows the inclusion of random effects in a Generalised Linear Model framework. The model structure is:

$$g\left(\mu_{ij}\right) = \mathbf{X}_i\beta + \mathbf{Z}_i\mathbf{b}_i + \mathbf{Z}_j\mathbf{b}_j + \mathbf{Z}_{ij}b_ij + \varepsilon_i, \tag{2.6}$$

where $g\left(\mu_{ij}\right) \equiv E\left(y_{ij}|\mathbf{b}_i, b_{ij}\right)$ and $y_{ij}|\mathbf{b}_i, b_{ij} \sim \text{Pois}\left(\lambda\right)$. Here, $\mathbf{X}_i$ and β are as previously defined in equation 2.5. $\mathbf{Z}_i$, $\mathbf{Z}_j$ and $\mathbf{Z}_{ij}$ are the random effects matrices for Year, Sector and Sector within Year respectively, and $\mathbf{b}_i$, $\mathbf{b}_j$ and b_{ij} are the associated coefficients, where $\mathbf{b}_i \sim N\left(\mathbf{0}, \Psi_1\right)$, $\mathbf{b}_j \sim N\left(\mathbf{0}, \Psi_2\right)$, $b_{ij} \sim N\left(\mathbf{0}, \sigma_3^2\right)$ and $\varepsilon_i \sim N\left(\mathbf{0}, \sigma^2\right)$. Here, $\mathbf{b}_1$ is characterised by Ψ_1, the variance-covariance matrix, which is defined to be symmetric and positive-definite. Ψ_1, which is termed Ψ, for generality, is formulated in terms of a relative precision factor, such that:

$$\frac{\Psi^{-1}}{1/\sigma^2} = \Delta^T\Delta \tag{2.7}$$

If Ψ is positive-definite, then there exists Δ, which is not necessarily unique. If the random effects are scalar, the variance of $\mathbf{b}_i$, σ_1^2 is a scalar. Thus, Δ is chosen to be $\sqrt{\sigma^2/\sigma_1^2}$. In this model, the random effects matrix is $Z_i^T = [1, 1, \ldots, 1]$, which is a scalar vector of length 18.

This is to allow the estimation of the sample taxon richness variability between and within lake sectors. Thus, σ_1^2 is a scalar, and the choice of Δ is trivial.

The GLMM structures are fitted using the Restricted Maximum Likelihood (REML) criterion. However, AICc is invalid when comparing models fitted with REML, if the fixed effects are different between the models. Therefore, the models will be fitted first using Maximum Likelihood (ML) and the final chosen model will be refitted using Restricted Maximum Likelihood (REML), in order to estimate the variance components more accurately. In order to take account of random effects, the equation below is maximised:

$$L(\beta,\vartheta) = |\Psi_\vartheta|^{-\frac{1}{2}} \int \exp\left(l(\beta,\mathbf{b}) - \frac{1}{2}\mathbf{b}^T\Psi_\vartheta^{-1}\mathbf{b}\right) d\mathbf{b}, \tag{2.8}$$

where Ψ is defined by the vector of variance parameters ϑ. The function is obtained by integrating out the fixed effects, β. The function $l(\beta,\mathbf{b})$ is the log likelihood calculated by treating the random effects $\mathbf{b}$ as fixed effects.

Model No.	Fixed effects	AICc	% Dev. expl.
1	MGD + TP + Sector + Year	2284.0	2.0
2	MGD + Sector + TP	2283.4	2.0
3	MGD + Sector + Year	2284.0	2.0
4	MGD + TP + Year	2280.4	0.6
5	Sector + TP + Year	2281.9	2.0
6	MGD + Sector	2282.7	1.9
7	Sector + TP	2290.0	1.5
8	MGD + TP	2278.9	0.5
9	**MGD**	**2278.3**	**0.5**
10	TP	2289.2	0.1
11	Intercept	2287.0	0.0

Table 2.9: GLMM models of the sample taxon richness data, with the AICc values and percentage of deviance explained given. As for the LM and GLM structures the deviance explained are calculated in relation to a null model. The null model for the GLMMs contains an intercept term for the mean with Year, Sector and Sector within Year as random effects. Model 9 is the chosen model.

Covariate	β est.	Std. Error	P-value
(Intercept)	0.10	0.11	-
MGD	0.18	0.03	<0.01

Table 2.10: Table of the MGD parameters from the chosen GLMM, with Sector as random effect.

Effect	Est. Std. Dev.
Year	$< 1 \times 10^{-4}$
Sector	0.11
Sector within Year	0.08
Residual	0.69

Dispersion parameter	0.59

Table 2.11: Estimated random effects and dispersion parameter in the chosen GLMM.

The models in table 2.9 are fitted using a log link function, as in the GLM setup. Model 9 has the best AICc value and is therefore chosen as the final model. MGD is the sole fixed effect covariate in the model and the MGD term is similar to the GLM result, with a slightly larger coefficient estimate in table 2.11.

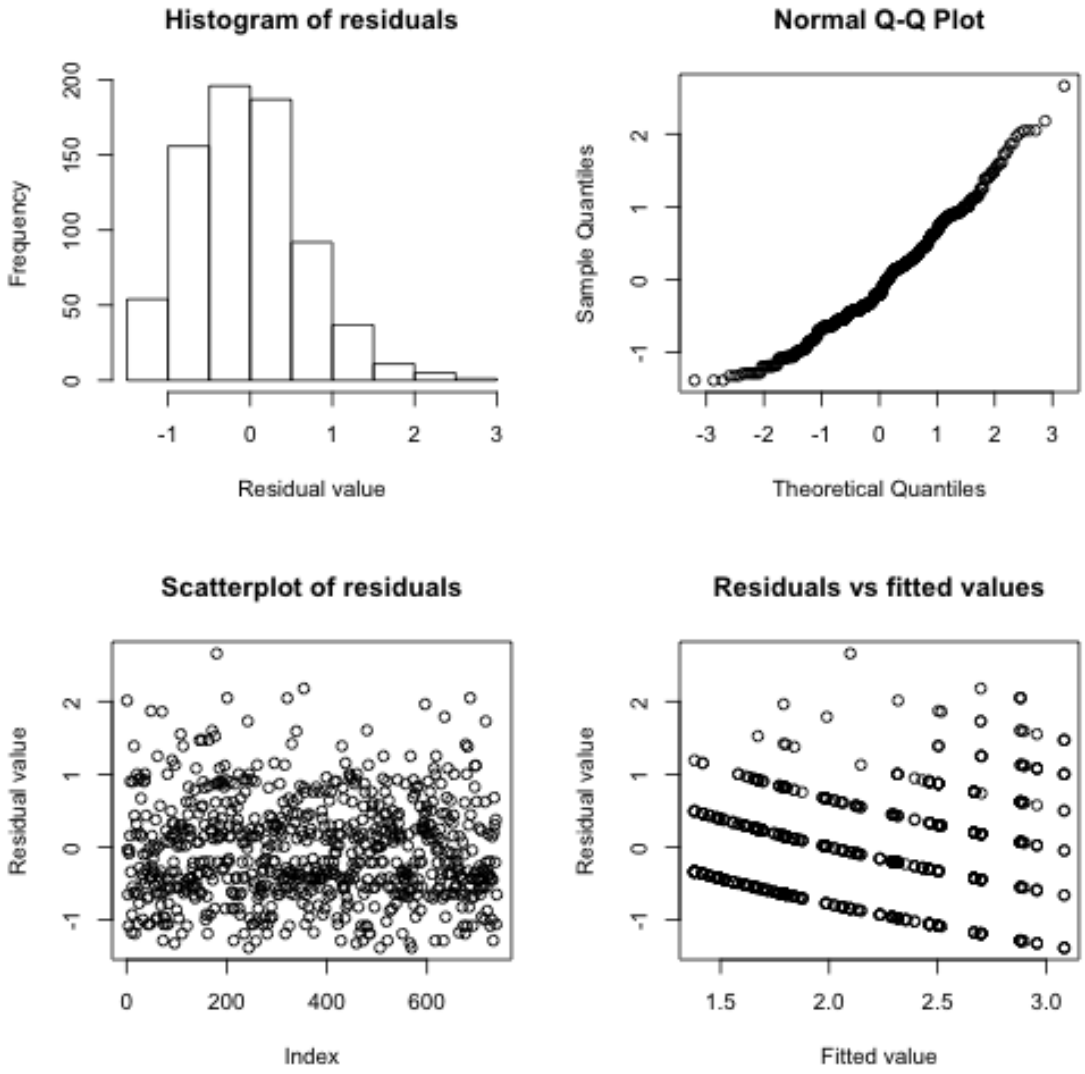

Figure 2.11: Diagnostic plots of the sample taxon richness generalised linear mixed model (GLMM), with Sector as random effect.

In relation to the GLM residual plots, the residual plots depicted in figure 2.11 appear to be slightly worse fitting with the histogram appearing relatively less skewed, but still show a slight deviation in the upper two plots. Given there is only one covariate in the final model, judgement as to the presence of heteroscedasticity in the residuals is difficult. The lower right plot of residuals against fitted values indicates slight heteroscedasticity; the lines emerging from this scatterplot are a facet of the count data, since there are only seven different responses in the data.

The effect of including Year, Sector and Sector within Year as random effects did change the final model: Sector is no longer included as a fixed effect, indicating that the differences between the defined 19 areas of the lake in terms of the sample species richness are not great enough to warrant the inclusion of the Sector covariate. The percentage of deviance explained by the model covariates is very small. The coefficient and associated standard error of the MGD covariate are estimated to be 0.18 and 0.03 respectively, whih are very similar to the chosen GLM. The random effect estimates for sector in table 2.11 shows that the estimated variation between sectors is greater than between years. However, the residual variability is much higher, six times larger than that between sectors. The very small standard deviation for Year as a random effect concurs with figure 2.9, showing that the variability between the mean sample species richness per survey is much smaller than the variability within surveys.

Given there is little information as to the position of each sample within each sector, it is difficult to estimate the variogram more precisely. The dispersion parameters in both GLM and GLMM structures in tables 2.8 and 2.11 indicate that there is underdispersion present in both selected models, but this is not deemed critical to the model itself. The absence of zeroes from the data may be one reason for this underdispersion, since the data appear to be censored below a response of 1.

2.3.6 Introducing spatial covariance

A spatial correlation structure is to be fitted to the residuals of the sample models; such a structure allows the relationship between the distance between response values and their correlation to be estimated. The exact position of the samples within each sector is not known. However, it is known that all transects begin at the lake edge. Thus the spatial position of the samples is taken to be the midpoint of the lake edge for each sector. This position is measured in kilometres. Due to the fact that two samples cannot be located at the exact same point, a very small random perturbation is added to the location of each sample, to avoid overlapping samples. The perturbation added to the data was tested for a number of different values and found not to affect the correlation function greatly.

A variogram cloud was calculated to show the semivariance between pairs of sample model residual values across the lake; the variogram cloud is shown in figure 2.12. From this image, the semivariance appears to be fairly constant with respect to distance. This indicates that

the correlation between samples across the lake is not dependent upon the distance between pairs of samples.

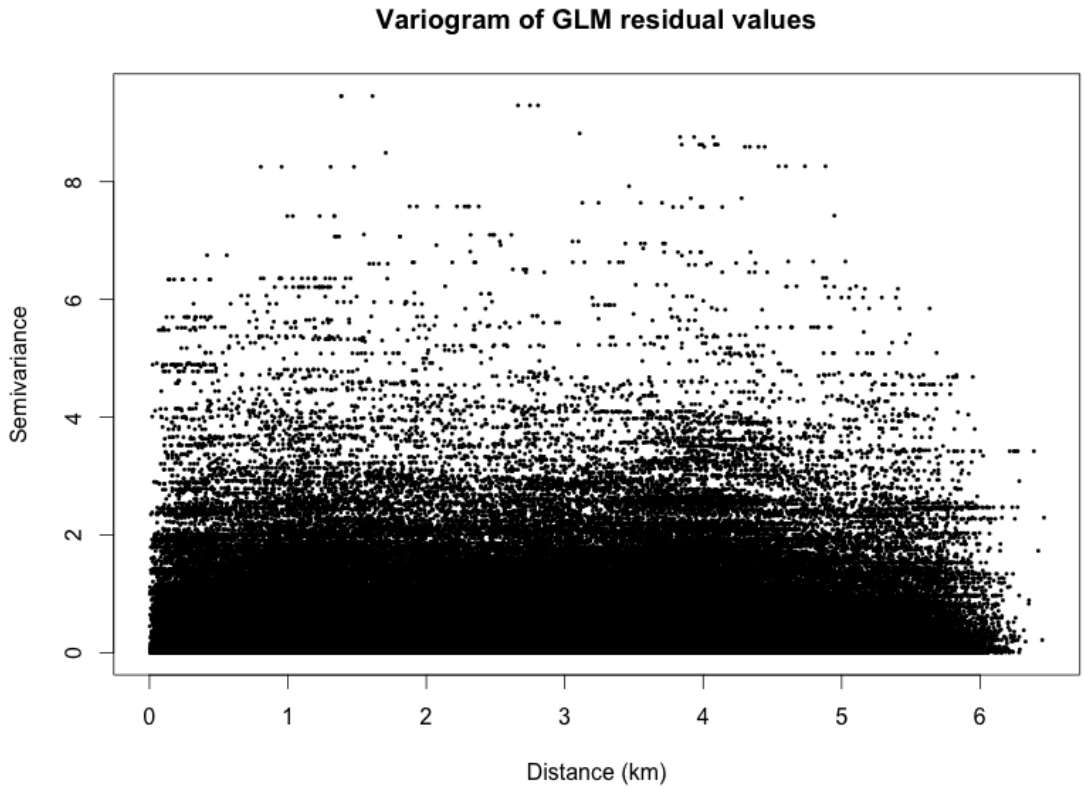

Figure 2.12: The variogram cloud calculated from the residualy of the GLM of sample taxon richness data.

In order to estimate what spatial correlation is present, a simple correlation function will be included in the GLM: the Gaussian function. The Gaussian correlation function is a simple correlation function to be used in this model, where the correlation between two values weakens, the greater the distance between those two points. The correlation function is as follows:

$$\rho(h) = \exp -\frac{h^2}{\phi} \tag{2.9}$$

Model	Nugget (τ)	Partial sill (σ^2)	Sill (s)	ϕ	Practical range (km)
GLM	0.46	1.54	2.00	22.44	38.85
GLMM	0.45	1.32	1.77	19.78	34.24

Table 2.12: Estimated parameters of the spatial correlation parameters for the Gaussian correlation model for the residuals of the selected GLM and GLMM.

where $\rho(h)$ is the correlation of the difference between two values distance h km apart, $h \to \infty$, and ϕ is the range parameter. The semivariogram can be calculated as:

$$\rho(h) = \sigma^2(1-\rho(h)) + \tau \mathbf{1}_{(0,\infty)}(h) \tag{2.10}$$

where σ^2 is the partial sill, $\rho(h)$ is the correlation function, τ is the nugget. The sill of the variogram, s is the sum of the partial sill, σ^2 and the nugget, τ. The practical range of the variogram is value of h at which the correlation between two samples is estimated to be equal to 0.05, i.e. when $\rho(h) = 0.05$. The described parameters are listed in table 2.12. The estimated range parameter, the distance at which the correlation between two values is 0.05, is much greater than the maximum distance across the lake. Other spatial covariance functions were tested and yield very similar results for the distance range under consideration.

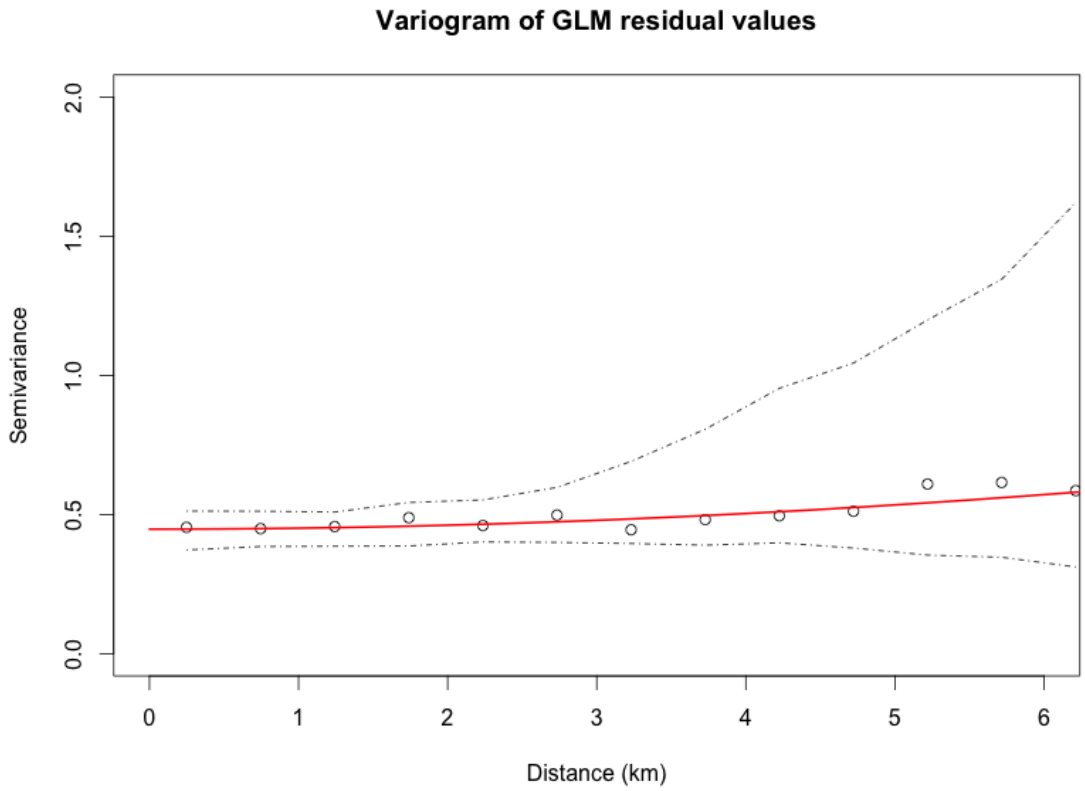

Figure 2.13: Graph of the binned variogram cloud values calculated from the residuals of the chosen GLM, with the Gaussian covariance function displayed. There is a slight variation in the binned semivariance values as the distance increases, with an fairly level towards a distance of 5km followed by a more marked increase between samples of just over 5km.

There is a slight increase in the covariance as the distance between the residual values increases in figure 2.13. However, the dotted lines which indicate the variogram envelope are very wide for distances above 5km and the other binned values are very similar. There were few samples which were at least 5km apart, hence the greater uncertainty associated at distances above 5km in for the estimated covariance function. Given the almost horizontal slope of the covariance function in figure 2.13 and the wide variogram envelope, it is inferred that there is very little spatial correlation between the GLM residuals. Due to the unknown specific location of all samples narrower than the sector, a better estimation of the nugget could not be made. A very similar covariance function was fitted for the GLMM residuals. The large nugget value of 0.45 and the relatively small change in correlation concur with the low standard deviation associated with the random effect of Sector in the GLMM.

Having analysed the data using multivariate and linear models, the results will be summarised and discussed along consequences for Loch Leven.

2.4 Discussion

2.4.1 Results of analyses

The multivariate analysis showed a change in the macrophyte population composition over time, and a return to a community more similar in makeup than the other surveys to that in 1905. The initial linear model showed that an increase in the max depth of macrophyte growth leads to an increase in the macrophyte lake taxon richness. Sampling strategies between surveys are not identical, and this may have influenced the number of different taxa recorded in the aggregate lake richness total. Approximately 50% more samples were made in 2008 than in the three preceding surveys. However, the length of samples is shorter in later years, so the overall sample area in more recent surveys may have actually decreased, despite the number of individuals samples increasing. This significant relationship between MGD and taxon richness is supported in the succeeding models.

The inference made in the linear model is reinforced in the Poisson GLM and GLMM, whereby the increase in recent years in fine-scale taxon richness is related to the maximum growth depth of macrophytes. Despite the greater number of samples in 2008, there has not been a dramatic change in the range of sample taxon richness for this year in comparison to the other three most recent surveys. In summary, it has been easier to assess change in recent years due to improved data collection and recording methods.

The spatial correlation of the response data was difficult to estimate, since no more local information on the location of the drag-rake samples was available than the sector in which they were recorded for all four most recent surveys. It is difficult to say whether the correlation structure estimated would have been different had the drag-rake sample locations been known very accurately. The random effect of sector affords an interpretation of the spatial variability within and between sectors across the lake; considerably more variation is present at the intra-sector level than inter-sector. This does not contradict the correlation structure range estimate, that correlation is not present between sectors.

In the selected GLM, the effect of MGD did not show an interaction with Sector, indicating that the sample species richness across the lake has the same relationship with the maximum growing depth of macrophytes. In the chosen GLM, Six sectors had positive significant coefficients in the GLM. Sectors 6 and 7 are between St. Serf's Island and the southeast shore of the lake. Sectors 11 and 12 are adjacent on the south shore and 15 and 17 are on the western shore. All these sectors could be considered more sheltered from the wind and the water is less turbid in these sectors and the water clarity is higher. This allows the macrophyte community to colonise a greater area. As a result, less nutrients are stirred up from the lake bed, meaning a lower nutrient concentration in the water and less eutrophic conditions. Competitive species do not then dominate so much and the taxon richness at the drag-rake sample level is higher.

Using the Poisson GLMM structure, the standard deviation of the Year random effect is relatively very small, indicating the variation within years is much greater than the variation between years. The covariate of Sector is no longer included in the final model as a fixed effect. The unexplained variability within each sector is much larger than that between sectors. Given the distances between samples within each sector, this is not unexpected. The reasons for the particular division of lake sectors in figure 2.3 are not known, but the locations of samples since 1986 have been recorded accurately.

By fitting Year and Sector as random effects, the AICc of the model containing Sector and MGD as fitted effects was marginally larger than that containing only MGD. Given the inclusion of the random effects, there are more model parameters than in the comparable GLMs; and as such the AICc is penalised more heavily. The deviance explained by the models was much smaller than the tested GLMs. This was due to the fact that the deviance in the null GLMM was much greater than in the null GLM. Given that only MGD was included in the final model, the sample taxon richness response is not considered to vary greatly between transects. This concurs with the standard deviation of the random effects, given the variability within Sectors is much greater than between Sectors.

The absence of zero values in the response data indicate that no areas of the lake were surveyed where macrophytes were not present. How intentional this result was is unclear. If samples in each transect were ended when no macrophytes were visible, this then infers truncated data and a biased sampling methodology. Given that there are no zeroes present in the response data, one cannot immediately infer from this that transects were discontinued due

to the absence of macrophytes; the transects could have been deemed to be long enough or their length determined prior to the sampling taking place. Absence of zero data therefore does not imply absence of macrophytes. Furthermore, since a sector in one year may contain differing numbers of drag-rake samples in different surveys, this is not necessarily evidence that the area colonised by the macrophyte population differed between surveys across that area of the lake. These models are created therefore for the studying of the taxon richness where macrophytes were known to be present. Evidence of the coverage across the whole lake cannot be made directly from the drag-rake samples or the maximum depth at which macrophytes were recorded. However, if one assumes that the maximum growing depth (MGD) of macrophytes in a given survey year is measured at the location of a drag-rake sample, then one can infer the the macrophyte population were at least as deep as this stated measurement. In which case, the MGD should be seen as a possible underestimation. A stated sampling method based on sample positions being chosen prior to the sampling taking place would allow greater clarity in interpreting the data and a more accurate understanding of the areas of macrophyte growth across the lake.

If the drag-rake samples are of equal length and equally spaced and one assumes that transects were continued until the macrophyte community was no longer present or visible along the transect line, then a greater number of samples in each transect would indicate a greater area of the lake bed inhabited by the macrophytes. This analysis has not considered the number of transects in each sector and survey, but a simple metric of the length of each transect would allow inference to be made on the area colonised by macrophytes within each sector. Unfortunately, without knowledge of the reasons fo halting a transect, such a method involves too many assumptions on the surveying techniques.

The low dispersion ratios showing underdispersion in the data indicate both the GLM and GLMM variances are greater than the data indicate, which in turn leads to overestimated standard errors associated with the coefficients. Part of the reason for this underdispersion is also probably due to the absence of zero values, resulting in the truncated range of responses. Overdispersion is more often considered a problem for Possion-distributed models in the literature, given that when it the data are overdispersed then the model coefficients are not as precise as the results maintain. However, since there is underdispersion in these models, this indicates the estimated model coefficients are more precise than the results show.

2.4.2 Statistical discussion

Having looked at the results of the models fitted, discussion will now be given to the statistical techniques employed in these analyses and any issues that have been encountered in the modelling process.

All the linear models have an intercept or categorical effect of Sector present; the only other fixed effect is MGD. Thus the Sector or intercept term is the estimated taxon richness where MGD is zero. However, given that no samples were recorded when the MGD was lower than 2 metres, the intercept is outside the range of the observations and no inference is made about the relationship between MGD and taxon richness below this value. Thus, the inclusion of these terms in the chosen models is justified.

The lake level is subject to fluctuation, due to changes in input and drainage control. Thus, if the level wer lowered, the size of the habitable area for submerged macrophytes would decrease, even though the observed MGD would not change, which would mean the deepest point in the lake which macrophytes are found to inhabit would have remained constant while the edges of the lake which were previously habitable could no longer be colonised by the macrophyte community. Likewise, if the lake level were raised, the position of the macrophyte colony may remain constant at the deepest points of the lake while the observed MGD would be greater. However, variability in lake depth across a period of sampling during August and September is much lower than the variability shown in MGD values recorded (May and Carvalho, 2010). Therefore such an occurrence is not deemed to have affected the results of the model.

Some taxa are better adapted to growing in deeper water, or can more quickly colonise uninhabited areas.The models that have been used do have some clear limitations. No generalised additive model (GAM) structure was used in the analyses, due to the lack of sufficient data to estimate smoothing splines accurately. However, the linear relationships in the results suffice for what data are available.

In comparison with the models with mean fitted for each model structure tested, there is no more than 35% deviance explained in the initial models tested and approximately 23% and 0.5% explained for the selected GLM and GLMM respectively. This shows there is still a

large amount of variability unexplained by the models. This is expected to an extent, since taxon richness is not expected to be uniform across the lake or each sector and apart from sector, the fixed effects are not available at a finer spatial level than at the whole lake. The final GLMM estimates the vast majority of this variability to be present at the within-sector level, indicating that there is comparatively less of a difference between the sample taxon richness values of each sector than within each sector. The inclusion of random effects increased the significance of the fit between MGD and sample taxon richness for every sector; the estimated between-sector variability is relatively small compared to within sectors.

The magnitude of potential errors in MGD and TP load covariates is unknown; the recorded MGD value may not be the absolute lake maximum, as there could be deeper plants that were undetected. Also, TP load estimates of phosphorus in-flow and bird populations may be inaccurate. However, the position of the sectors within the lake are well-defined so all transects are assumed to be associated with their true sector.

There could be an argument for pseudo-replication in the GLM in tables 2.7 and 2.8, given that there is only one value of MGD per survey year and multiple samples per sector and survey. However the covariate of MGD appears in the GLMM as well, where Year and Sector within Year are fitted as random effects. The coefficient of MGD is slightly greater in the GLMM than in the GLM and still significant at the 5% level but with a increased associated standard error.

The effect of transect could have been included as random in the model setup, nested within Sector. Given transects extended out perpendicular from the lake edge, there is great variability in the lake depth within most transects, resulting in differences in taxon richness between the drag-rake samples. As such, the variation within transect may have been greater than between transects within each sector.

The TP load and MGD covariate values used in the regression models were measured in the same year of each survey. However, given that changes in the level of TP loading may have a delayed effect on the macrophyte community, more regular measurements of these variables are suggested in order to test for the presence of a lag effect, as well as predicting sample taxon richness by measuring the MGD. These measures would not be very labour-

intensive and could help with testing for a lagged relationship between nutrient loading and the macrophyte community.

Sampling

In the linear model, an aggregate taxon richness total was used as the response. The number of samples made in each survey has not remained constant over time; from 1905 to 1975 the figure is unknown, as is the length of each individual sample before 1993. For the surveys where samples were made with a drag-rake from a moving boat, it is thought that the length of these samples was at least 2 metres, i.e. longer than the length of the boat. The samples in 1986 were each at least 5 metres. If a linear relationship exists between the natural logarithm of the sampling effort and the number of taxa recorded, then one can account for any potential bias by dividing the survey taxon richness by the logarithm of sampling effort (MacArthur and Wilson, 2001). There is a general increase in this figure for the most recent four surveys (table 2.13). This trend concurs with the increase in sample taxon richness witnessed in the generalised linear models (Figure 2.9), which occurred as sampling effort decreased. Therefore it is inferred that a bias based on sampling distance is not present. As the distance of each sample in the 1986 survey was not regular, the total sampling distance for that survey is the number of samples (165) multiplied by the minimum sampling distance, which is 825 metres. In the other three surveys, the distance that the drag-rake was pulled through the water for each sample was 2 metres.

Survey	Distance sampled (metres)	Taxon richness	Taxon richness/log(Distance sampled)
1986	825	10	1.49
1993	300	11	1.93
1999	340	10	1.72
2008	512	15	2.40

Table 2.13: Relationship between taxon richness and distance sampled for the latest four surveys. Although the number of samples in the 2008 survey was greater, the minimum total distance of all samples was not as great as in the 1986 survey.

This problem of bias in sampling effort is not considered an issue in the GLM or GLMM structures, as the length of the drag-rake samples in the latest three surveys are smaller than those made in 1986, yet an increase in the sample taxon richness in recent years is witnessed,

as depicted in figure and 2.9. A trend is obtained linking species per sample with the MGD recorded in these later surveys. If samples in 1986 were only collected by a 2 metre pull of the drag-rake underwater, the taxon richness in each sample may be smaller still, and the positive trend over time would be increased. Thus the recorded change in sample taxon richness is conservative.

The presumption is that in the 1986 survey the drag-rake was pulled through the water until it was full, and then the taxa were recorded. The lengths of the samples in 1986 are probably indicative of thickness of the submerged foliage, i.e. it was not as thick as in later years: 1993 onwards. However, given this method, it is not known whether similar results would have been obtained over short distances, since the distance of each individual sample in earlier surveys is not recorded. If the exact distance of each sample in 1986 were known, the taxon richness per sample could be plotted against the distance for the samples in each sector. This trend could then be extrapolated back to estimate the taxon richness for samples of only 2 metres in length.

The exact position of all samples was not known, and as a result was not included in the model. This would have allowed for a more accurate estimation of the spatial correlation across the lake. Sampling of the same positions in subsequent surveys would allow for better comparability between surveys and would allow for the change in the macrophyte community dynamic at the sample level to be estimated more precisely. The length and position of the drag-rake samples in each transect should be defined prior to beginning sampling. They should also be long enough to include positions in the lake where there are no macrophytes, in order that the data are not artificially truncated to include no zero values.

A more intensive collection of data, where the mass of each taxon in each sample were recorded, would benefit the calculation of more complex biodiversity indices to be used as the model response. Presence-absence in each sample is recorded in the latter four surveys. The mass of each taxon could be regarded as a surrogate measure of abundance, thus allowing indices based of abundance to be calculated for each sample.

Accurate GPS measurements could be used for the position of each sample in transects, in order to allow spatial mapping of the data, with the potential usage of the bathymetric map to include depth at each sample position as a covariate in the regression model. Certain species

of macrophyte may be more sensitive to lake conditions such as depth than others. Besides the sample depth, fish and wildfowl could be used as explanatory covariates. Estimates of annual fish species populations which eat macrophytes, and numbers of geese which deposit phosphorus into the lake, would allow these potential fluctuating effects to be measured. Thus, the accurate mapping of individual taxa would be advantageous in assessing lake condition more precisely, by reference to their preferred conditions.

Sampling via the use of a drag-rake is inherently invasive, since taxa must be removed from their habitat in order to be identified. Although there were not many comprehensive surveys available for this analysis, if such observations are carried out too often, the macrophyte community may not have sufficient time to recover after each survey. It is assumed that the surveys at Loch Leven were temporally far enough apart in order to allow the recovery of the community to pre-sampling levels. Given the increase in the mean sample taxon richness over the period of the latest four surveys, the surveying method is not considered detrimental to the macrophyte community. In the 2008 survey, a bathyscope was used to identify the macrophyte taxa present at specific locations, in order to avoid disrupting the plants. This method of sampling is more labour-intensive than using a drag-rake and may thus not be suitable for use across the whole lake or where the water is deeper and therefore darker.

2.4.3 Ecological discussion

The maximum growing depth of macrophytes is an indicator of the area which is inhabited by the macrophyte community and thus the clarity of the water (light levels) and nutrient levels. It is not necessarily indicative of the 'health' of the macrophyte community *prima facie*, only that some macrophyte taxa have been able to colonise the lake to a certain depth. From the models, the MGD is inferred as a driver of change, but this is only a surrogate of the true drivers, of which TP loading is suspected to be the largest driver of change. Also, the leaching of phosphorus into the lake from sediment does not occur at the same time as the loading of phosphorus into the lake. Hence, there is a difficulty in the use of TP loading estimates in the model. The TP concentration at time of survey is not always helpful in explaining macrophyte community behaviour May and Carvalho (2010). Nevertheless, in the analyses presented in this chapter, a link is established between the present conditions as indicated by MGD, i.e. how deep macrophytes have been recorded, and how diverse the macrophyte community is. The inclusion of Sector as a categorical covariate in the GLM

shows the importance of location in defining differences in sample taxon richness. It is not known how taxon diversity varied across the lake before eutrophication, but it is not necessarily expected that the response would be uniform.

Consequences for Loch Leven

An increase in maximum depth of macrophyte growth has led to greater diversity in the macrophyte population. This measured change in MGD is viewed as a proxy measure of the cleanliness of the lake itself, and in turn of the recent lake TP concentration. Thus, the decrease in phosphorus load is seen as initiating an increase in the habitable area. The increase in lake taxon richness shown in the linear model since the 1960s could potentially be solely due to this increase in area and broadening of the available ecological niche for the macrophyte community. Moreover, sample taxon richness is shown to have increased in recent years in the Poisson Generalised Linear Model. Thus, not only are more taxa found in the lake a whole, but taxon richness within each drag-rake sample has increased since 1986.

With the inclusion of Sector as a random effect, the estimated variability at the sub-sector level is relatively greater than between sectors. This is also seen in the poor spatial correlation across the lake. Variation between sectors could be explained by coarser measures such as the size of the fetch for each sector. The fetch is a measure of the distance that air travels over open water across a lake. A larger fetch could create more turbid conditions, stirring up sediment from the lake bed, thereby reducing light levels in the water column and thus inhibiting macrophyte growth. Other lake activities such as fishing may be driving spatial and temporal macrophyte variability. Spatial analysis of the colonised area for each taxon would allow interactions between taxa to be better understood.

As discussed earlier with regard to the Alternative Stable State theory, the lake system potentially needed to be cleaner than it was in 1905 to return to near such a position of health in the macrophyte community, since following the theory, a greater ‘perturbation’ is necessary to return to the initial state that was required to move out of the initial state. The known change in TP loads, although not significant in the models, is cited as the cause of eutrophication and the subsequent recovery. Present sources that contribute to nutrient loading in the lake are not expected to decrease greatly in the foreseeable future. Therefore the possibility

of nutrient levels falling low enough for species richness to start decreasing and the lake to become oligotrophic (Figure 2.1) is not a present concern.

In light of the multivariate analysis and initial model concerning the taxon list within each survey across the whole lake, there is a perceived change in the taxa recorded. However, certain species which were found in the 1905 survey were not found in any other surveys until 2008, for example *Potamogeton praelongus*. Thus, it is thought that this species probably never left the lake system but was just lower in number and distribution, and thus not always visible in the intervening surveys. Some species such as *Potamogeton lucens*, only recorded in the earliest survey, may have disappeared entirely, and if so, it will be difficult for them to recolonise within the lake, given its isolated location from other macrophyte colonies. Therefore, it is conceded that the system may never be exactly as it was approximately 100 years ago. What is achievable is a healthy system, as measured by MGD, according to the WFD (2000). If the maximum growing depth of macrophytes is regarded as being an indicator of healthy conditions, then this analysis has shown that it is also a good estimator of the taxon richness of macrophytes, both at the whole lake and fine-scale sample levels.

Despite the difference in the sampling lengths previously discussed, a recovery in sample taxon richness since 1986 is still recorded. If the data up to and including 1986 were recorded using the same methodology as post-1986, detailing which taxa were found in which sample, then it would be possible to gain a better understanding of the change in the macrophyte community during eutrophication in the 60s and 70s.

The results in this analysis support the hypothesis by Dudley et al. (2012) that the witnessed recovery in the macrophyte community is attributable to the lake recovery from eutrophication, and shows that the maximum growing depth of macrophytes as a 'state' is an indication not only of recent TP loads into Loch Leven, but also explains the variability in the taxon richness of the community. This result concurs with work by May and Carvalho (2010), which infers the same process at Loch Leven and also the Lake Fure study by Sand-Jensen et al. (2008) in Denmark.

This witnessed recovery in taxon richness in Loch Leven is attributed to improved water quality. However, one could also use information on the individual species to infer general conditions in the lake; this could be conducted by reference to species' known preferred

nutrient and light levels. For instance, inferring lake condition by reference to the preferred trophic status of macrophytes species recorded, was made by Nurminen (2003) in a study of a Finnish lake. However, given that it is accepted that Loch Leven has recovered from eutrophication, as indicated by MGD, it is more interesting to note how the diversity changed over this time. As has been suggested already, with a reduction in the area of the lake bed available to the macrophyte community to grow, more competitive species dominated the habitable regions and thus the recorded taxon richness decreased across the lake, as well as at a fine-scale level. In relation to future pattern of driver behaviour, it is not expected that TP loads will increase. The MGD level may yet increase, if TP loading remains stable, which may lead to a further increase in macrophyte taxon richness.

In summary, macrophyte communities can be severely affected by changes in nutrient loading to a lake system. The community response is not always uniform between locations, but recovery of taxon richness at the lake level is achievable, once nutrient availability decreases to remain consistent at previous levels of enrichment. Fine-scale, sample-level recovery is also possible, although it may be dependent upon other local environmental factors, both biotic and abiotic.

External nutrient loading to the lake is still considered to be problematic. Brownlie et al. (2014) assess a new methodology for controlling phosphorus inputs to Loch Leven from private sewage systems. Internal nutrient loading can also be reduced by the application of phosphorus capping materials, such as bentonite clay, which has been found to increase the capacity of the lake bed to adsorb dissolved phosphorus and reduce its release into the water column (Gunn et al., 2014). Further reduction of nutrient availability in the water column can aid the continual recovery of Loch Leven from eutrophication.

The analysis conducted in this chapter has contributed to evidence of the change in the macrophyte community over a period of over 100 years as well as the link between the condition of a lake as indicated by the MGD and the taxon richness of the macrophyte community which inhabits the lake. Lakes such as Loch Leven may have stronger spatial correlation between the taxon richness found in observations across the lake, but there has been no evidence found of strong correlation in the data available. In order to explain more of the variability in the macrophyte response, finer-scale information is needed on the spatial variability of lake conditions.

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Chapter 3

Carabids

3.1 Introduction

Biological communities such as carabids (*Coleoptera: Carabidae*, ground beetles) often have a large degree of spatial and temporal variability (Lövei and Sunderland, 1996). In this study, samples of carabid populations at 10 terrestrial sites in the Environmental Change Network (ECN) are used to study the change in community structure over time, at single sites and across the network. This will enable inferences about the impact of environmental pressures on the beetle communities and the extent to which these pressures are driving spatio-temporal variability in the beetle community. Looking initially at two sites from two different environments individually, single-site models of the beetle response are fitted using two different indices, before fitting multi-site models for the same responses at ten of the twelve ECN terrestrial sites. This introduction outlines characteristics of carabid communities with regard to their activity as a response to environmental pressures.

There are hundreds of different species of carabid which occur in many habitats across Great Britain, present in varied assemblages. There are approximately 150 different genera and 350 species of *Carabidae* found in Great Britain. In this dataset, the different carabid species measure in average length from under 5 to around 40 mm. They are mostly nocturnal and generally disperse across the ground in the soil-litter interface, rather than in the vegetation layer (Maudsley et al., 2002). Certain species, e.g. *Trechus quadristriatus* have wings enabling flight and others, e.g. *Calathus melanocephalus* are wing-dimorphic, meaning some individuals of that species have the potential to fly while others have their wings

fused together. Species have separate breeding periods, in spring, summer or autumn, though some species are able to change the period in which they breed according to suitable conditions.

Carabids have relatively short ranges of activity over the course of a day; Baars (1979) record the mean distance travelled per day of radioactive-tagged *Pterostichus versicolor* individuals as varying between 4 and 14 metres and *Calathus melanocephalus* individuals between 1 and 4 metres. With the aid of a meta-analysis Brouwers and Newton (2009) estimate the median distance travelled by carabids to be 2.1 metres per day. They also observe a positive. correlation between the body size of carabid species and the distance travelled each day The area covered by each species over the course of a season is estimated to be 1-2 hectares for *Pterostichus versicolor* and 9-12 hectares for *Calathus melanocephalus*. Baars (1979); van Dijk and den Boer (1992).

There are many known benefits of carabids to the environment, for example they act as pest control in agricultural areas as predators of other insects which damage crops. Some species prey upon snails, earthworms, caterpillars, butterflies, herbaceous plant seeds and of the larvae of larger insects (Deuve et al., 2012; Serić Jelaska et al., 2014; Honek et al., 2003). They are also themselves prey for larger species, such as moles, shrews and birds. They can aid in the pollination of plant species, and help the biodegradation of leaf dry-matter.

Sampling the activity density of carabids in a certain region or habitat can be seen as a surrogate measure of the carabid population as a whole in that area. Significant change in the numbers of beetles collected in these samples, either spatially or temporally, can be understood as a change upon particular species or the beetle community as a whole in that ecosystem.

There could be a shift in beetle numbers sampled at sites where beetle numbers are generally low as there is a risk that the trapping methodology significantly affects the beetle numbers. Pitfall traps are an invasive sample method; all beetles that are recorded in the samples are removed from the population at the time of capture. If the removed or “harvested” beetles are too many, relative to the population size, then it could adversely lower beetle numbers in the habitat. If certain taxa have a higher propensity of being caught, due to being smaller in size or more active than others, then the community balance within a certain transect could

be disturbed. However, variability in carabid communities over is considered to be greater than trapping pressure and the number of carabids caught is not greatly affected by removal of individuals through trapping (van Dijk and den Boer, 1992).

Koivula (2011) discusses the usefulness of carabids, as indicators of change in environmental pressures. It is noted that anthropogenic drivers such as pesticide usage may effect short-term reductions in beetle density in an impacted region. Heavy metal deposition is also reported to have a significant negative impact on carabid populations; cadmium and zinc deposition, for instance, have been negatively linked with the growth of a certain species, *Poecilus cupreus* (Koivula, 2011).

There is no strong conclusion on the effect of soil moisture on carabid densities. Some studies have observed a positive correlation between soil moisture and and species richness (Antvogel and Bonn, 2001; Sroka and Finch, 2006) whereas some species have recorded opposite effects in response to spatial variation in soil moisture (Holland et al., 2007). Larvae of *Calathus melanocephalus* are observed to be dependent upon soil moisture content during the winter period being within a certain range, with both extreme dryness or wetness considered dangers to their survival (van Dijk and den Boer, 1992). Winter precipitation changes followed by increased nitrogen deposition are cited as having an indirect effect upon beetle communities. Both pressures lead to plant species such as heather to be invaded by more ruderal grass species, leading to large-scale land management changes to cut the foliage, which could harm the beetle population dramatically (van Dijk and den Boer, 1992).

Daily temperature has a positive effect on beetle activity and hence on the number of beetles captured in many different environments (Honek, 1997; Saska et al., 2010, 2013). Beetle populations can show responses to other land management, such as controlled burning. It was found that both the number of beetles and carabid species richness were negatively affected by burning, but the effects of such events were short-lived and not detrimental in the long-term to the beetle population in that area (Willand et al., 2011).

Studies involving the effect of nitrogen deposition on carabid communities have shown a positive correlation with the number of beetles caught, but a negative correlation with diversity (Raworth et al., 2004; Batáry et al., 2008). This indicates that certain species benefit more from the increased nitrogen deposition. Sulphur deposition is considered to have a detri-

mental effect on carabids and negative responses in the number of individuals observed in carabid communities have been recorded as a result of increase in sulphur deposition.(Rybak, 2009)

Habitat heterogeneity and disturbance as pressures upon beetle populations have been studied by Vanbergen et al. (2005). Using species richness and beetle abundance as the response data in multivariate analysis, it was concluded that the species richness and abundance of beetles were greatest in the most heterogenous habitat landscapes.

Carabid sampling schemes in the literature are often conducted for a limited time period and focus on a single location or small number of sites. There are few long-term studies on carabids, which allow for analysis of the community response over an extended period of time.

Scott and Anderson (2003) consider the inter-annual fluctuations in beetle populations and differences between species composition in different habitats in the ECN over eight years of survey; indicator species are promoted to be used as the model response, in assessing the health of particular communities. Fluctuations in summary statistics such as the diversity of a beetle community are subject to large variation across years. As such, it is difficult to describe trends in the population in terms of environmental changes. They suggest that in order to observe changes in the beetle population at a site, it is advantageous to calculate the diversity of annual beetle catches on only dominant species, rather than creating an index based on the whole community. Scott and Anderson (2003) also suggest however that species which are low in number but widespread at many sites should be monitored also, inferring their sensitivity to climate change. The network of sites and the sampling methodology are described below.

Other taxon assemblages, although they may impact on each other within an ecosystem, have been studied as separate responses to environmental drivers and pressures, such as birds (Buckland et al., 2008; Freeman and Newson, 2008), butterflies (Roy et al., 2001; van Swaay et al., 2008) and bats (Walsh and Harris, 1996; Kaňuch et al., 2008) Given the variety of statistical analyses used in such studies, there is no defined approach to analysing spatio-temporal change in a taxon group such as carabids. Understanding of spatio-temporal variability within the beetle community is therefore important when comparing the changes

within such groups and identifying overarching changes that may be affecting multiple taxon groups.

Up to this point, there has been discussion of beetle population sampling and possible reasons for the response of individuals to spatio-temporal changes in the environment, as well assessment and modelling of other taxon groups which require bespoke sampling schemes. Attention is now turned to the modelling of beetle communities in the ECN itself.

3.1.1 The ECN sites

The sites in the ECN which are used in this analysis are summarised in table 3.1 and how long the beetle transects have been in operation; figure 3.1 shows the location of the ten sites in the analysis. Cairngorm, Glensaugh, Moor House, Snowdon and Sourhope are considered upland sites, with minimum altitudes of 137 metres (Table 3.1).

Site	Min. Alt. (m)	Max. Alt. (m)	Site area (ha)	Start year
Alice Holt	110	125	850	1994
Cairngorm	320	1110	1000	1999
Drayton	40	80	190	1993
Glensaugh	137	487	1125	1994
Moor House	290	848	7500	1993
North Wyke	120	180	250	1993
Rothamsted	94	134	330	1992
Snowdon	298	1085	700	1999
Sourhope	200	601	1119	1994
Wytham	60	165	770	1993

Table 3.1: Details on all sites used in the analysis, displaying the range of altitudes at each site; the site area and the first year of sampling.

Figure 3.1: The location of the ten Environmental Change Network sites in the analysis, created using Google Earth.

3.1.2 Beetle sampling in the ECN

Beetles in the ECN were sampled using pitfall traps: receptacles sunk into the earth, so that the rim was level with the ground. The beaker was half-filled with anti-freeze: a solution to trap the beetles, but one that will stay fluid in cold conditions. A cylindrical wire mesh was inserted into the beaker, to prevent small mammals and birds from entering the trap, and disturbing the sample. A secure lid was attached to prevent flooding via precipitation. Gaps in the mesh were wide enough for the beetles to fall through; the trap therefore captured any beetle that crossed the wire mesh threshold.

Other methods for sampling in the beetle population exist besides pitfall trapping, such as window traps, used to catch beetles mid-flight, or emergence traps, bottomless cone-shaped structures which are set into the humus layer of the soil (Huber and Baumgarten, 2005) Some of the ECN sites are located in very remote areas, where extreme weather conditons may lead to more delicate traps being damaged and data being lost as a result. Hence robust structures such as pitfall traps are needed. Beetles can also be sampled via soil samples or mark-recapture methods (Lövei and Sunderland, 1996), both of which are very labour-intensive.

Within each site, beetles were sampled in 3 line transects, comprising 10 pitfall traps in each, positioned 10 metres apart. The traps are emptied every fortnight for at least 26 weeks every year approximately from May to November; the number of individuals of each species in each trap is recorded. A fourth transect was installed at Moor House in 2000; Cairngorm and North Wyke had short-term transects installed in 2006. There are incomplete data records for certain sites: Drayton for 2006, Rothamsted for 2000 and Snowdon for the period 2006 to 2008, inclusive. Hillsborough and Porton Down are not included due to problems with the environmental covariate data at those sites, leaving ten sites for analysis.

Trap methodology is constant between and within sites, meaning that changes in response are not due to differences in the sampling method. In order for a supposed spatial or temporal gradient in activity of a population to be recorded by the traps, the activity density must first occur within the locale of the transects. Movement a short distance from the transect will not be seen. Secondly, if the beetle is to be caught, it must fall into a trap.

The activity of certain taxa in different habitats may differ, and so the results obtained via this method may be skewed towards the more active species in those particular environments. Larger beetles have a theoretically smaller chance of falling in, since if behaviour between species with regard to barriers is similar, they are more likely to collide with a vertical wire and divert their path. With these concessions, the trap catch does give an idea of the extent of a population's diversity. Absence from the sample does not imply absence from the population, but presence in the sample (however active a certain taxon is considered to be) automatically determines presence in the population. Thus, when counting the number of taxa in a habitat, the sample is a minimum of the number of taxa present.

Morecroft et al. (2009) examine the changes in the log total of all beetles and the species richness at each ECN site over the sampling period. A generalised linear model is fitted in order to assess changes in the sampled beetle response at each site. The caught beetles are aggregated to the site and year level; a linear trend of year is fitted for each site. An AR(1) model is also fitted to correlate the within-site errors, so that the error term at a given site in year t is correlated with the error term for the year $t-1$. A significant decline in species richness was recorded at Cairngorm, Drayton and Snowdon (also known as Yr Wyddfa) sites. A significant positive trend was observed at Porton Down. In modelling the log total trend of beetles, a highly significant decrease in the number of individual carabids trapped was observed at Cairngorm; no other significant trends were observed.

3.1.3 Aim

The aim of the analysis is to describe the relationships between the response of the beetle community and the model covariates. Environmental pressures will be sought which best describe the witnessed trends between beetle populations over time and between sites and habitats. In so doing, it is considered what environmental effects may be driving the beetle population and what is causing spatial differences in biodiversity, as measured by activity density.

Since the publication of the study of dominant species' trends in the ECN by Scott and Anderson (2003), five more years of long-term survey have been added to the data which are used in this case study, which can aid in the understanding trends in the biodiversity of the beetle communities within the network. In analysing data from multiple sites, the trends

observed by Morecroft et al. (2009) will be fitted against environmental covariates, in order to explain changes in the biodiversity between sites and across years.

The carabid data are implemented as the response in a Generalised Linear Mixed Model framework, with environmental covariates to assess if, and to what degree, spatial and temporal changes in the diversity of the carabid population can be attributed to measured environmental pressures.

3.2 Beetle diversity

The beetle response is complex; there are many different beetle species, which are trapped in vastly different numbers, within and between sites. As discussed in section 1.3, when analysing changes in a community over space, it is important to know what change is measured. Totals of only the dominant species, as suggested by Scott and Anderson (2003), which are recorded at a certain transect do not provide information on the increase or decrease of rarer taxa, that may have the potential themselves to become dominant or that may be more sensitive to environmental drivers and pressures. By concentrating on a single species, a large amount of information on the intra-community dynamic is lost. By using an index based on the abundance of each *genus* in the community, a more complete community response is created, while being invariant to changes in intra-*genus* abundance and therefore more robust than an index based on *species* abundance.

Two responses are calculated: log total and Shannon-Wiener index. Due to the exponential trend in beetle activity noted at some sites over the course of a sampling season, the log of the total number of beetles caught is used, following the response used by Morecroft et al. (2009). The data are highly positively skewed, so taking the natural logarithm of these values results in the removal of this skewness while still being easily interpretable. The Shannon-Wiener index, as described earlier in chapter 1 will be tested also, in order to take into account both genus heterogeneity and evenness in the model response. In comparison to the species richness as a response, the Shannon index takes into account both the heterogeneity and evenness of the community, which will increase when there is less dominance of the community by a few genera or a single genus.

Specialists and generalists may respond differently to environmental change and may have different impacts on the community indices. The genera *Pterostichus* and *Amara* are both prevalent at Rothamsted, but their relationship to the community as a whole is not completely clear. numbers of the generalist *Pterostichus*, at the Transect-Month scale, show a negative correlation with the transect diversity index (Figure 3.2). There is greater range in diversity for lower values of *Pterostichus* abundance. However, the genus is clearly able to be active in large numbers in all three transects at this site. Focussing solely on the activity in *Pterostichus* does not explain the variability in the Shannon index when *Pterostichus* activity density is low.

The *Amara* genus on the other hand is regarded as more of a specialist. Rutledge et al. (2004) study the use of such beetles as a management tool against pest control. The *Amara* genus is trapped in relatively higher numbers in the grass transect (Figure 3.3). In the grass habitat, a lower number of individual beetles are captured for the whole community where the *Amara* genus are greater in number. However, there is no clear relationship visible for the arable and forest transects, perhaps as the numbers trapped here are considerably lower (Figure 3.3).

To focus on only modelling generalists, such as the *Pterostichus* genus, would remove the influence of such genera as *Amara* on the community response. Conversely, in only modelling specialist genera where they are perceived to dominate, such as *Amara*, the overall response of generalist genera is lost. Furthermore, each *genus* can only be modelled in the habitats in which they occur. The modelling of single genera that are dominant at a given point in time assumes that the activity density of those genera is not dependent upon other genera which have the capacity to become dominant also. Neither of the genera profiled in figures 3.2and 3.3 can explain the variability in the community response, when they are lower in number themselves. Thus, the response chosen to be modelled is that based on the whole carabid community.

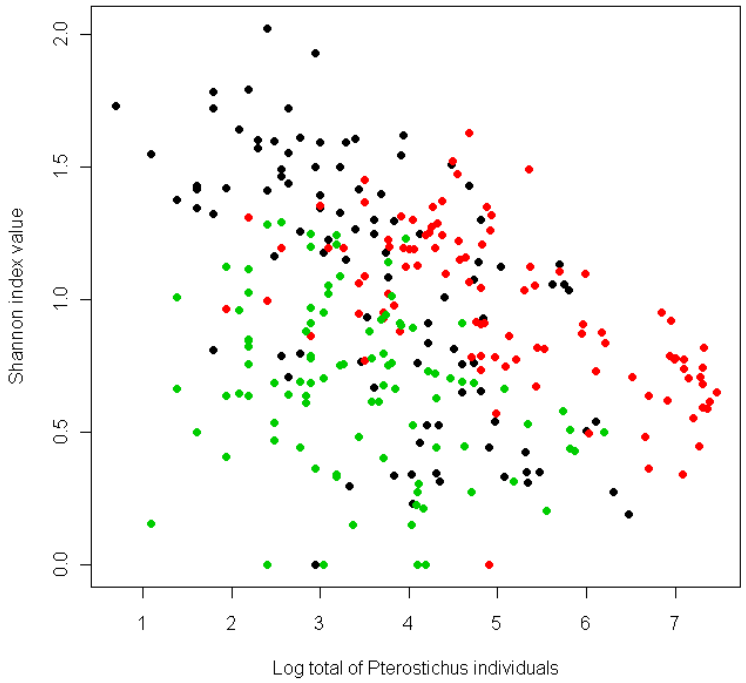

Figure 3.2: Scatterplot of the Shannon index value and numbers of *Pterostichus* beetles trapped in each transect and month period at Rothamsted. Colours denote the different transects: black = arable transect, red = forest transect, green = grass transect.

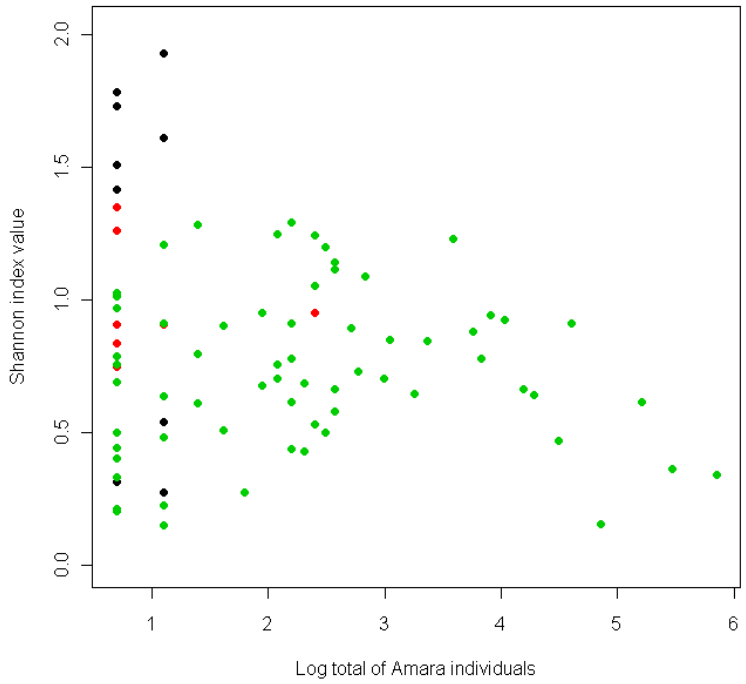

Figure 3.3: Scatterplot of the Shannon index value and numbers of *Amara* beetles trapped in each transect and month period at Rothamsted. Colours denote the different transects: black = arable transect, red = forest transect, green = grass transect.

Several spatio-temporal beetle responses can be used, based on the different aggregations of the data. When a beetle falls in a specific trap in a given fortnight, its entry time is not known. The Trap-Fortnight response is the finest scale univariate response possible. Initially the data will be aggregated by site and year. Some simple analyses will be conducted in order to look at the long-term trends before splitting the beetle response data by transect and then by month. The environmental covariates will then be included and their ability to explain the variability in the index responses will be assessed.

3.3 Long-term trend analyses

Following on from the long-term trend analysis in Morecroft et al. (2009), 10 of the 12 ECN sites are to be analysed with respect to the log total of individuals and the Shannon index of the samples. There appears to be greater variation in the log total of beetles caught between the sites than between the years within each site (Figure 3.4).

As previously stated, only the ten sites shown in figure 3.1 and table 3.1 are used. Following Morecroft et al. (2009), the data are aggregated by Site and Year and a GLM is fitted with a linear trend estimated for each site. A mixed model framework will be fitted as follows:

$$I_{ik} = \alpha_k + \beta_k Y + e_{ik} \tag{3.1}$$

where I_{ik} is the index in Year i and at Site k, α_k is the intercept at each site and β_k is the slope associated with Year for each site k; separate trends are fitted for each site. As also performed by Morecroft et al. (2009), an AR(1) structure is fitted in the model, in order to the estimate the correlation within sites over the years. The error term e_{ik} at time i and site k is fitted as:

$$e_{ik} = \phi e_{i-1,k} + q_{i,k} \tag{3.2}$$

, where $e_{i-1,k}$ is the residual value at year $i-1$ at a defined site k, ϕ is a constant where $-1 < \phi < 1$ and $q_{i,k}$ is a random process, normally distributed with mean 0 and variance σ_Q^2. The estimated value of ϕ is the reported in the tabled results. A value of ϕ close to 1 would indicate high positive correlation between the error terms and the error term from the previous year at the same site; a value close to -1 would thus indicate high negative temporal auto-correlation.

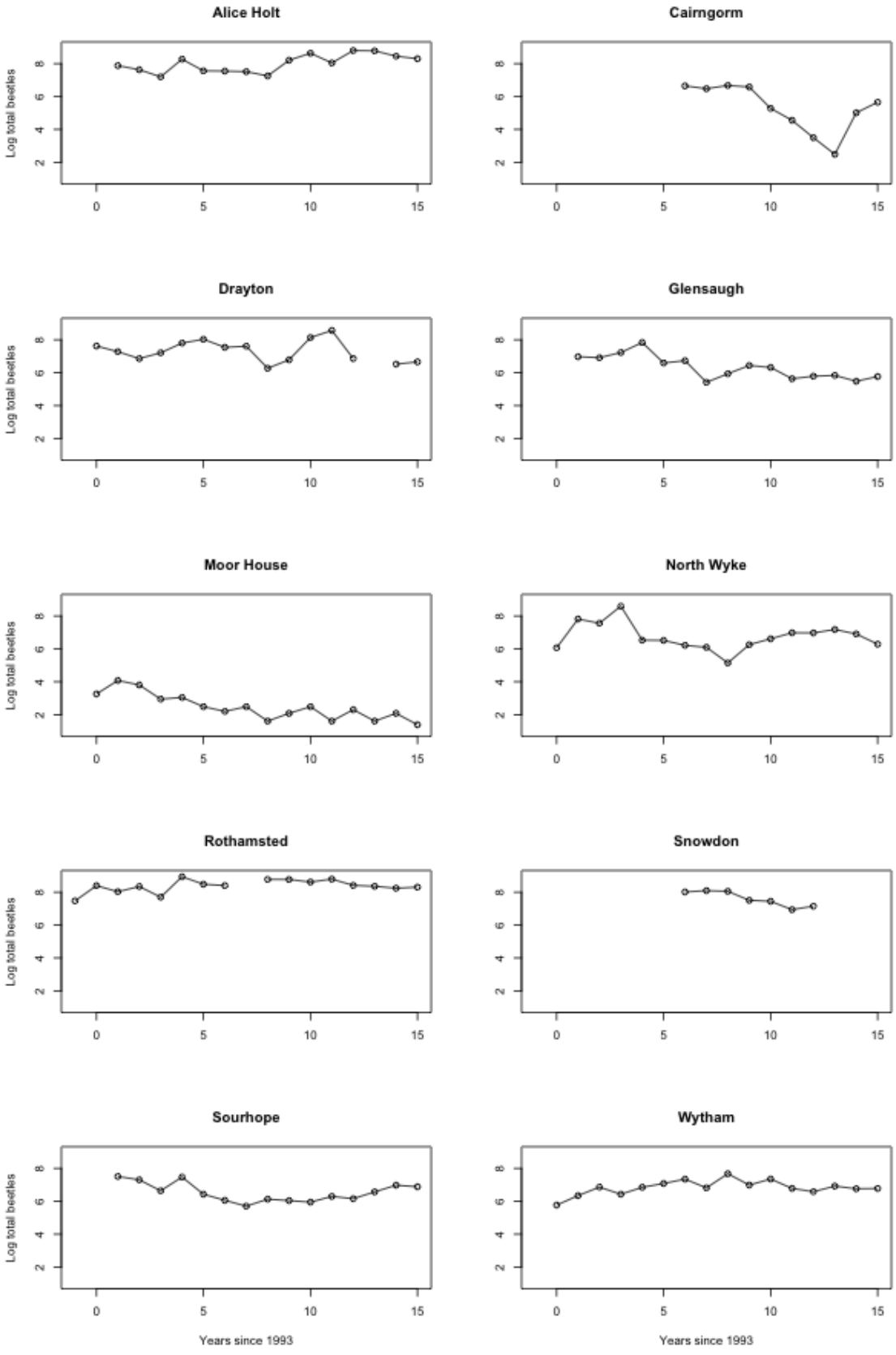

Figure 3.4: Plots of the annual log total of beetles caught at 10 of the 12 ECN sites, for the three long-term transects at each site only.

	Log total			Shannon index		
Intercept	Estimate	Std. error	P-value	Estimate	Std. error	P-value
ALI	7.53	0.60	<0.01	0.85	0.29	<0.01
CAI	7.64	0.1.16	<0.01	0.70	0.57	<0.01
DRA	7.62	0.54	<0.01	1.76	0.26	<0.01
GLE	7.21	0.60	<0.01	1.99	0.29	<0.01
MOO	3.54	0.54	<0.01	1.39	0.26	<0.01
NOR	6.79	0.54	<0.01	2.45	0.26	<0.01
ROT	8.06	0.48	<0.01	1.60	0.24	<0.01
SNO	9.09	1.51	<0.01	0.86	0.74	<0.01
SOU	6.99	0.60	<0.01	2.64	0.29	<0.01
WYT	6.41	0.54	<0.01	1.42	0.26	<0.01
Slope	Estimate	Std. error	P-value	Estimate	Std. error	P-value
ALI:Year	0.06	0.06	0.34	-4.42×10^{-3}	0.03	0.89
CAI:Year	-0.21	0.11	0.05	0.08	0.05	0.12
DRA:Year	-0.05	0.06	0.41	-0.01	0.03	0.74
GLE:Year	-0.11	0.06	0.09	-9.56×10^{-4}	0.03	0.98
MOO:Year	-0.13	0.06	0.02	-0.03	0.03	0.32
NOR:Year	-0.02	0.06	0.76	6.05×10^{-3}	0.03	0.83
ROT:Year	0.04	0.06	0.48	-0.03	0.03	0.21
SNO:Year	-0.17	0.16	0.31	-0.05	0.08	0.50
SOU:Year	-0.04	0.06	0.49	-0.03	0.03	0.36
WYT:Year	0.05	0.06	0.43	-1.62×10^{-3}	0.03	0.95

AR(1)	Log total	Shannon index
ϕ	0.57	0.58

Table 3.2: Trends by site and year,with the data aggregated by site and year. Site names are: ALI - Alice Holt, CAI - Cairngorm, DRA - Drayton, GLE - Glensaugh, MOO - Moor House, NOR - North Wyke, ROT - Rothamsted, SNO - Snowdon (Yr Wyddfa), SOU - Sourhope and WYT - Wytham.

From table 3.2, the log total model shows significant negative trends across Years at the 5% level are at Cairngorm and Moor House. Slight positive trends at Alice Holt, Rothamsted and Wytham. All other estimated Year coefficients are negative. The Moor House trend is in contrast to that estimated by Morecroft et al. (2009), where only a very slight trend is observed and it is not significant. Moor House had a fourth transect added in 1999; this served to increase the number of traps being sampled over the season from 30 to 40. The model in table 3.2 used only data from exactly three transects at each site. The lack of any

clear negative trend in the log total response at that site in the analysis by Morecroft et al. (2009) may be due to the inclusion of the fourth transect data.

Almost all trends in the Shannon index were negative; none of these were significant. The only positive trends estimated were at Cairngorm and North Wyke; given that there was a significant negative trend in the log total model at this former of these two sites, the two trends may be linked if dominant genera saw greater proportional reduction in numbers of individuals caught, which would lead to the Shannon index increasing over time as the log total decreased.

Including the AR(1) correlation structure in the model means that the responses at each site are assumed to be dependent upon the previous year's response at that site. The AR(1) estimate for both models is very similar, with estimates of ϕ of 0.57 and 0.58 for the log total and Shannon responses respectively. This indicates that there is reasonably high correlation at each site over time for both responses.

The site indices are, as previously explained, the aggregation of beetles caught in three transects, which are often located in very different habitats at each site; these individual transects could exhibit very different responses. The transects are also positioned far enough apart such that each transect can be considered as a sample of an independent beetle community. Thus, the variability in the beetle samples can be analysed by aggregating the data to the transect level in each site and year. This means there are now three responses at each site in each year instead of just one in model 3.1. Given that the transects within each site are often in differing habitats, there are potentially differing trends for each transect. By using this finer scale of sampling, the overall trend over time in individual habitats may differ from those trends observed in table 3.2.

In equation 3.1, Site is treated as a fixed effect. In this way, the sites are treated as being of intrinsic interest and the individual trend at each site is estimated. However, Site can also be considered as a random effect in the model instead. This method assumes that the sites themselves are representative of the beetle population in Britain. It is conceded that the site locations were not in fact randomly selected, but chosen for a wide variety of reasons. they represent a range of locations, habitats and environments within Britain. By treating Site as a random effect, they are thus considered to be representative of the country-wide beetle

population. However, certain habitats are omitted from the sites; urban and coastal sites for instance. As such, overall trends may be biased agains these habitats.

An overall linear trend for Year will be fitted for all sites. However, Year is fitted as a random effect also, in order to take account of the pseudoreplication, given there are multiple measures at each site in each year. Site is nested within Year as a random effect in order to estimate the standard deviation between sites within years. The model fitted is as follows:

$$I_{ikl} = \alpha + \beta Y + \mathbf{Z}_i \mathbf{b}_i + \mathbf{Z}_k \mathbf{b}_k + \mathbf{Z}_{ik} b_{ik} + e_{ikl} \tag{3.3}$$

where I_{ikl} is the index in Year i at Site k in Transect l. An overall trend of Year is fitted with an estimated coefficient β associated with it and an intercept term α. The random effects of Year, Site and Site within Year are denoted by the matrices $\mathbf{Z}_i$ and $\mathbf{Z}_{ik}$ with vectors of coefficients $\mathbf{b}_i$ and b_{ik} respectively. The coefficients are normally distributed, where the $\mathbf{b}_i \sim N\left(0, \sigma_1^2\right)$, $\mathbf{b}_k \sim N\left(0, \sigma_2^2\right)$ and the $b_{ik} \sim N\left(0, \sigma_3^2\right)$.

	Log total			Shannon index		
Covariate	Estimate	Std. error	P-value	Coefficient	Std. error	P-value
(Intercept)	5.63	0.51	-	1.43	0.18	-
Year	-0.04	0.01	< 0.01	-0.01	< 0.01	0.01

Random effects S.D.	Log total	Shannon index
Year (σ_1)	$< 1 \times 10^{-4}$	0.02
Site (σ_2)	1.60	0.55
Site within Year (σ_3)	0.39	$< 1 \times 10^{-4}$
Residual	0.85	0.42

Table 3.3: Trends by site and year with data aggregated by transect and year, with an overall trend of Year and random effect of Year, in order to account for pseudoreplication within Year.

In table 3.3, the coefficient of Year is slightly negative and significant at the 1% level for both responses. The estimated standard deviation of the random effects show that the variation between years is very small compared with the variation between sites. The variation between sites within years is much smaller than for the main effect of site for both responses. In both models the standard deviation at the site level is larger than the residual standard deviation; for the log total model it is nearly twice as large as the residual value.

In order to analyse the trend within years in more depth, the next aggregation will be at the transect and month level. This will allow the seasonal trend for the period which the beetles are surveyed to be analysed. Two of the ECN sites will be analysed in detail: Rothamsted and Sourhope, which are two sites with very different beetle responses. The chosen model structure will then be extended to all ten sites in the previous models.

3.3.1 Rothamsted

Rothamsted was founded as a research centre in 1843 and it has sites for the study of sustainable land management in various habitats. The transects at this site are less likely to be subject to unknown changes in land use over their period of sampling. Therefore, changes in the activity density of the carabid population may be more directly related to broad environmental changes in drivers and pressures, rather than fine-scale change as a result of land management.

The time series plots of the Shannon index of each Rothamsted transect are depicted in figures 3.5, 3.6 and 3.7. There is a gap in the sampling history, since no samples were made in the year 2000. The same traps were used after the sampling history interlude. There is a clear strong seasonal trend in the data; in most years, there is a drop in the index value in the middle of each sampling season. The index values range from 0 to approximately 2, with with the arable transect having a slightly larger range than the other two transects. There does not appear to be any clear trend of increasing or descreasing index values over the complete period of survey (Figures 3.5, 3.6 and 3.7.

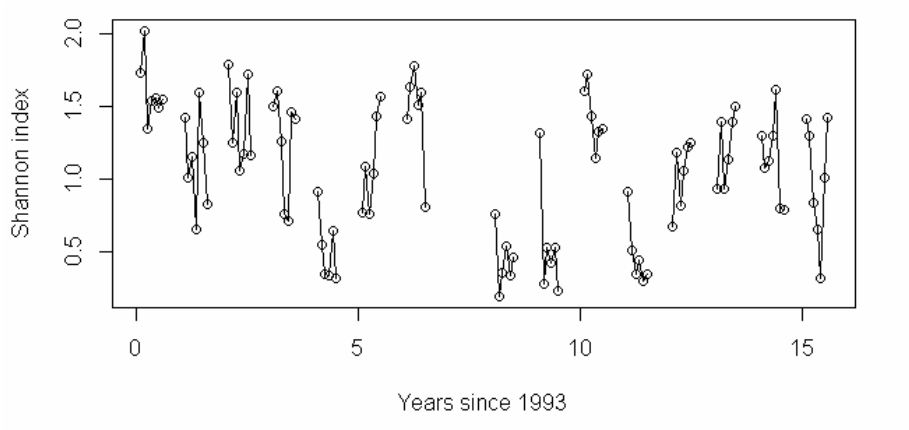

Figure 3.5: Time series of Monthly Shannon index values for the arable transect at Rothamsted.

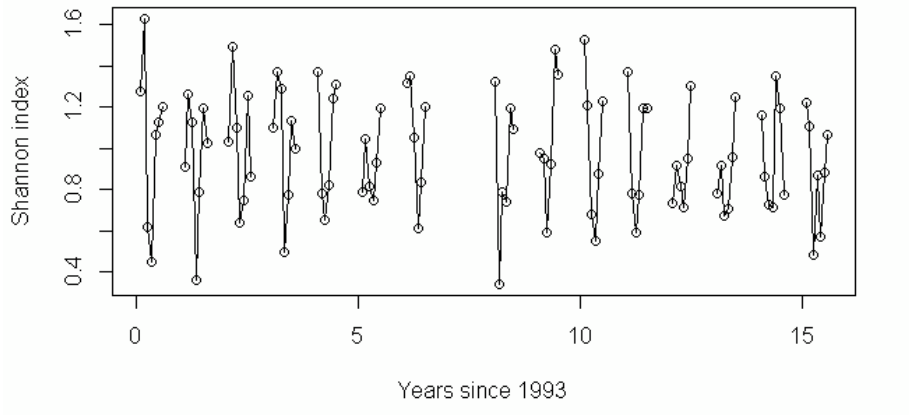

Figure 3.6: Time series of Monthly Shannon index values for the forest transect at Rothamsted.

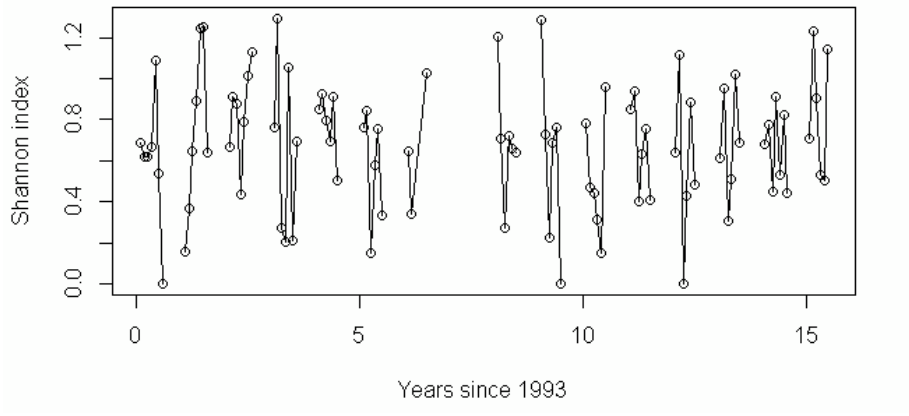

Figure 3.7: Time series of Monthly Shannon index values for the grass transect at Rothamsted.

In order to analyse the trends within each year and transect, the data are aggregated to transect-month level. Month is the new factor to be included in the model. Like the covariate of Site, Month can be included as a fixed or random effect. As a random effect, the variation within and between months within each year can be estimated. As a fixed factor, the seasonal trend would be captured by the model, as a separate coefficient would be fitted for each month of survey. Separate models will be fitted and assessed, with Month as a random effect and then as a fixed effect. In fitting Month as a random effect, the following model of the beetle samples at Rothamsted is fitted:

$$I_{ijl} = \alpha + \beta Y_i + Z_i \mathbf{b}_i + Z_j \mathbf{b}_j + Z_{ij} b_{ij} + e_{ijl} \tag{3.4}$$

where the response I_{ijl} is calculated for the ith year, jth month, and lth transect. Year (Y) is fitted as a linear trend as in equations 3.1 and 3.3, with coefficients β associated with Year and an intercept term, α. Year is fitted as a continuous covariate in order to detect a potential trend across years. Month is fitted as a random effect in order to estimate the variation between months within each year. This within-year variability is considered appropriate, given there are no data at the beginning and end of each year, forming a natural break within the Year groups. Year is fitted as a random effect again as in equation 3.3, due to the pseudoreplicated data within each year. The random effects of Year, Month and Month within Year are denoted by the matrices $\mathbf{Z}_i$, $\mathbf{Z}_j$ and $\mathbf{Z}_{ij}$ with vectors of coefficients $\mathbf{b}_i$, $\mathbf{b}_j$ and b_{ij} respectively. The coefficients are normally distributed, where the $\mathbf{b}_i \sim N\left(0, \sigma_1^2\right)$, $\mathbf{b}_j \sim N\left(0, \sigma_2^2\right)$ and the $b_{ij} \sim N\left(0, \sigma_3^2\right)$.

	Log total			Shannon index		
Covariate	Coef. Est	Std. error	P-value	Coef. Est.	Std. error	P-value
(Intercept)	4.48	0.34	-	0.99	0.06	-
Year	0.01	0.01	0.44	-0.01	0.01	0.16

Random effects S.D.	Log total	Shannon index
Year (σ_1)	$< 1 \times 10^{-4}$	0.09
Month (σ_2)	0.85	0.11
Month within Year (σ_3)	$< 1 \times 10^{-4}$	$< 1 \times 10^{-4}$
Residual	1.03	0.37

Table 3.4: Model of Rothamsted data only, aggregated by transect, year and month. The response data which are used to fit the Shannon index model are depicted in figures 3.5, 3.6 and 3.7.

In table 3.4, the linear trend of Year is are very small for both responses; the trend is slightly positive for the log total model and slightly negative for the Shannon index model. Both trends are non-significant as for the Rothamsted trends in model 3.2. There is therefore no great discrepancy between the coarse-scale trend of Site and Year-aggregated data and the finer-scale Transect and Month level. The standard deviation for the random effect of Year is very small, as in table 3.3. The estimated variation between months within years is very small also. The standard deviation for the main random effect of Month is much greater than between years, indicating the variability across months is greater than across years. It can also be seen that the residual variation, between transects within months, is greater than the variability between months. No AR(1) structure is fitted in this model, given that Year, Month and Month nested within Year are fitted as random effects and the correlation structure is designed only to estimate the within-group correlation.

The factor of Month can also be fitted as fixed, in order to estimate the mean value of the beetle index response within the sampling season and the standard error of the term for each separate month. Year is still fitted as a linear trend in the model structure, which is as follows:

$$I_{ijl} = \alpha + \beta_1 Y \; + \; \beta_{2j} M_j + Z_i \mathbf{b}_i + Z_l \mathbf{b}_l + Z_{il} b_{il} + e_{ijl} \tag{3.5}$$

where the response I_{ijl} is calculated for the ith year, jth month, and lth transect. Month (M) is included as a categorical factor and Year (Y) as continuous, with coefficients β_1 and $\beta_2 = \left(\beta_{2,5}, \ldots, \beta_{2,11}\right)$. Year is fitted as a continuous covariate in order to detect a potential trend across years. Month is included as a factorial covariate in order to estimate a parameter for each month separately, since the seasonal trend within each year is not linear. The random effects of Year, Transect and Transect within Year are denoted by the matrices $\mathbf{Z}_i$, $\mathbf{Z}_l$ and $\mathbf{Z}_{il}$ and vector of coefficients $\mathbf{b}_i$, $\mathbf{b}_l$ b_{il}, to estimate the variation between and within transects, where the $\mathbf{b}_i \sim N\left(0, \sigma_1^2\right)$, $\mathbf{b}_l \sim N\left(0, \sigma_2^2\right)$ and $b_{il} \sim N\left(0, \sigma_3^2\right)$.

In the model in equation 3.5, Transect is treated as random in the following model; the assumption is made that the transects themselves are representative of the beetle population at each ECN site. An AR(1) model is fitted as the correlation structure between the residual errors. It is often the case that there are months of samples missing between the end of one sampling season and the beginning of the next season. Indeed, there are only 7 months of survey at the Rothamsted site. In this case, the AR(1) correlation structure is contained within each transect within years, since the random effects grouping cannot be smaller than

the correlation grouping. The error term e_{ijl} in Year i, Month j and transect l is fitted in the correlation structure as:

$$e_{ijl} = \phi e_{i,j-1,l} + q_{ijl} \tag{3.6}$$

where $e_{i,j-1,l}$ is the residual value at Month $j-1$ in Year i in the defined transect l, ϕ is a constant where $-1 < \phi < 1$ and q_{ijl} is a random process, normally distributed with mean 0 and variance σ^2_Q. The estimated value of ϕ is the correlation reported in table 3.5. The random effects grouping is Year and Transect within Year. As in model 3.1, the AR(1) structure does not estimate the correlation between years, so the correlation between the last month of sampling in Year i and the first month of sampling in Year $i+1$ for any given transect is not taken into account.

The results of the models fitted as in equation 3.5 are displayed in tables 3.5; the linear effect of Year is non-significant in both models. Month is significant, as could be expected from the strong seasonal trend in figures 3.5, 3.6 and 3.7. As the log total Month coefficient is greatest in months 7 and 8, so the Shannon index is smaller in this period. This indicates the dominance of one or a few genera, causing the diversity of the community to fall. The random effects for the log total model in table 3.5 show the estimated standard deviation between years to be very small. This variability between transects within years is estimated to be smaller than for the main effect of Transect in the log total model, but very similar for the Shannon index model. For the Shannon index model, the residual variation within transects is larger than the variation between transects. The magnitudes of the random effect standard deviations between the models are not immediately comparable, due to the response values having different distributions. The estimated residual correlation parameter, ϕ, in both models is very small: 0.09 and 0.03 respectively. This indicates the temporal autocorrelation for the Shannon index is stronger than for the log total index. Both values are much smaller than for the Site by Year model reported in table 3.2, suggesting that the autocorrelation is weaker when within-site and seasonal variability is taken into account.

	Log total			Shannon index		
Covariate	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Year	0.01	0.01	0.35	-0.01	0.01	0.17
Month 5	4.02	0.54	0.01	1.11	0.14	<0.01
Month 6	4.92	0.54	0.01	1.09	0.14	<0.01
Month 7	5.03	0.54	0.01	0.82	0.14	0.01
Month 8	5.86	0.54	0.01	0.78	0.14	<0.01
Month 9	4.44	0.54	0.01	1.02	0.14	<0.01
Month 10	3.82	0.54	0.01	1.06	0.14	<0.01
Month 11	3.20	0.56	0.01	0.93	0.15	<0.01

Random effects	Log total	Shannon index
Year (σ_1)	$< 1 \times 10^{-4}$	$< 1 \times 10^{-4}$
Transect (σ_2)	0.91	0.20
Transect within Year (σ_3)	0.13	0.19
Residual	0.69	0.28
AR(1) ϕ est.	0.09	0.03

Table 3.5: Mixed-effects model of the Rothamsted Transect-Month models. The data which are used to fit the Shannon index model are depicted in figures 3.5, 3.6 and 3.7. In contrast to the models in table 3.4, Month is fitted as a fixed factor instead as a random effect. This model structure will be used to test the effect of environmental covariates on the model responses.

Exploratory models have been fitted to the response data for ten sites and for a single site. The appropriate scale of response has been explored also with the variability between responses at spatial and temporal scale assessed. In the single site model, the appropriate structure is assessed. By fitting Month as random, the variability between months is estimated. By fitting Month as fixed, as in table 3.5, the seasonal trend is taken into account. In exploring what variation in the response can be explained by environmental drivers and pressures in addition to the seasonal trend in the beetle response, Month is chosen to be fitted as a categorical covariates. Thus the model structure in equation 3.5 will be the basis for the fitting of environmental covariates to the response in the next section.

3.4 Effect of environmental pressures

Up to this stage in the analyses, only Year, Month, Site and Transect have been fitted as model effects. By including selected environmental pressures in the models, the ability of these new covariates to explain variability in the response can be observed and therefore possible causal links between the pressures and the beetle response can be inferred.

3.4.1 Explanatory covariates

In fitting Month as a fixed factor, the seasonal trend in the response is fitted by estimating an intercept term for each month. The changes in the beetle population which cannot be explained by the intra-year trend or are more appropriately explained by other covariates to be correlated with the environmental information collected at each site and month.

Time Series plots of some environmental covariates at Rothamsted are displayed in figures 3.8, 3.9 and 3.10. Figure 3.8 shows the monthly average rainfall estimates; here is large intra-year variability witnessed in many years, with no clear pattern and with no definite trend between the years. Rain can be considered a surrogate measure of soil moisture to which, as previously mentioned, beetles in arable habitats have been shown to have varying responses (Antvogel and Bonn, 2001; Holland et al., 2007). The response of a biodiversity measure, such as the Shannon index, to soil moisture is not clearly understood. If, for instance, dominant genera responded positively to increased soil moisture with an increase in activity, one would expect the Shannon index to decrease, due to a decrease in the evenness of the beetle community. If all genera respond positively to soil moisture, the Shannon index may not be affected; if rare genera respond positively, the Shannon index may increase.

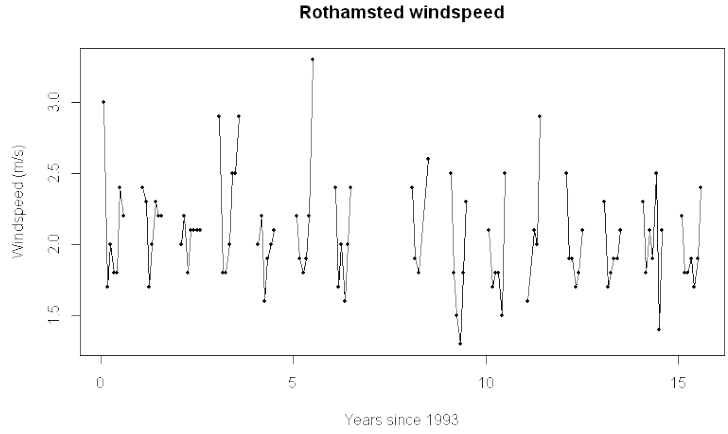

Figure 3.9: Monthly mean of hourly windspeed measurements in metres per second at Rothamsted, over the main trapping period from April to November.

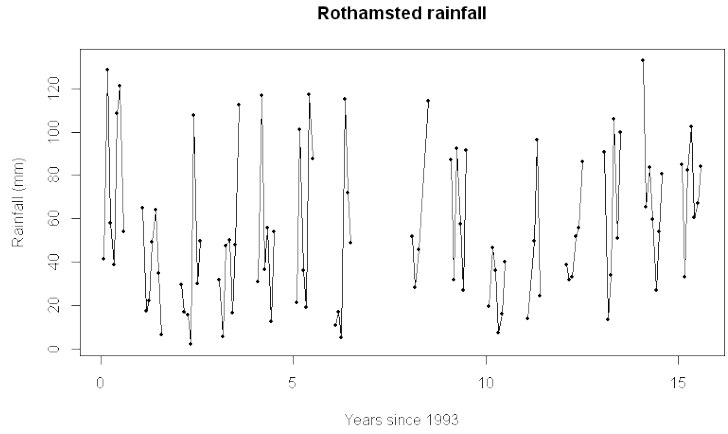

Figure 3.8: Monthly total rainfall measured in milimetres per month at Rothamsted, over the main trapping period from April to November.

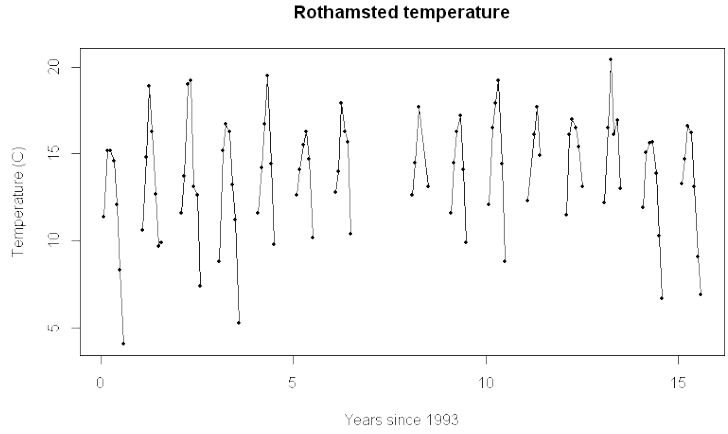

Figure 3.10: Monthly mean of hourly measured temperatures in degrees celcius at Rothamsted, over the main trapping period from April to November.

The trend for temperature shows a reasonably symmetrical parabola over the sampling period within each year (Figure 3.10). There does not appear to be a trend for increasing temperature over the period of survey. Peak temperatures generally occur in July and August, with peaks in each year of at between about 15 and 20 degrees. Temperature is considered to have a positive effect on beetle activity and thus on the number of beetles caught overall (Honek, 1997; Saska et al., 2010, 2013).

Scatterplots comparing the model responses with environmental covariates at Rothamsted are shown in figures 3.11 and 3.12. The covariates are the same for the three transects, taken from monthly measurements at the Rothamsted site. The covariates measured are: Rain (total milimetres per month), Temperature (°C, mean of hourly measurements per month), Wind speed (m s^{-1}, mean of hourly measurements per month), deposition of nitrogen as Nitrate-nitrogen and sulphur as Sulphate-sulphur (mg l^{-1}, total per month, volume weighted). Nitrogen deposition is considered to have a positive effect on the number of beetles caught (Raworth et al., 2004; Batáry et al., 2008), whereas sulphur is considered to have a negative effect (Cárcamo et al., 1998; Sroka and Finch, 2006).

Reduced nitrate and sulphate deposition have been shown to reduce the leeching of base cations in a woodland habitat, leading to the preservations of nutrients in the ecosystem (Boxman et al., 2008). Thus a reduction in nitrate and sulphate deposition may encourage growth of ruderal plant species in the region of interest. A increase in nutrient availability, as stated by van Dijk and den Boer (1992) with respect to the invasion of grasses in a heathland

environment. This quick growth in ruderal plant species can then result in necessary management changes to cut back the foliage, which can negatively affect the carabid population. Thus, there may be a indirect effect of deposition.

Windspeed measurements are shown in figure 3.9, where greater monthly averages occur generally at the beginning and end of the sampling season. Windspeed is not considered to have a direct effect on the beetle population. However, it is negatively correlated with air pressure and thus could be an indicator of extreme weather events during the period of observation, which may negatively affect beetle activity, for example due to water-logging, leading to a reduction in the log total number of beetles caught. A reduction in the Shannon index of the sampled beetles may occur if rarer and more specialist genera are not able to cope with changes in conditions and as a results are less active during bad weather, leading to more greater dominance observed in the beetles caught.

From figures 3.11 and 3.12, there does not appear to be any strong correlation between the covariates and the two responses respectively; there is also no clear relationship between the response variables themselves. However, correlations at the month level may become apparent when the seasonal trend is fitted with the fixed factor of Month.

The reasoning behind the possibility of the environmental covariates explaining variation in the responses is as follows: for a certain site, a change in a given environmental driver effects a change in the conditions for the transects placed there. Soil moisture, for instance, would be affected by rainfall; These changes may benefit or hinder certain genera according to their individual ecological niches and whether they are towards the centre or edge of the niche respectively. Subsequently, there may be a rise or fall in the number of beetles of those genera present in that transect area and active in that location, leading to a change in the chance that they may fall into the traps and be recorded.

Habitat is not fitted as an effect in this initial model, since Transect is reported at the same level, and thus confounded with, Habitat. Fitting Habitat as a fixed factor would have allowed the differences in habitat means to be estimated, thus allowing the effect of differing plant populations or land management schemes on the beetle population to be considered.

Given that the covariates of rainfall, temperature, windspeed, nitrogen and sulphate deposition are all measured each month at the single positions in each site, there is no finer-scale information which could explain variability between transects. As can be seen in table 3.4, for both model responses, the standard deviation associated with Transect within Month and Year is much larger than the standard deviations for Year or Month within Year. It is these large proportions of variability which cannot be explained by the covariates and will lead to a large percentage of deviance unexplained by the selected models.

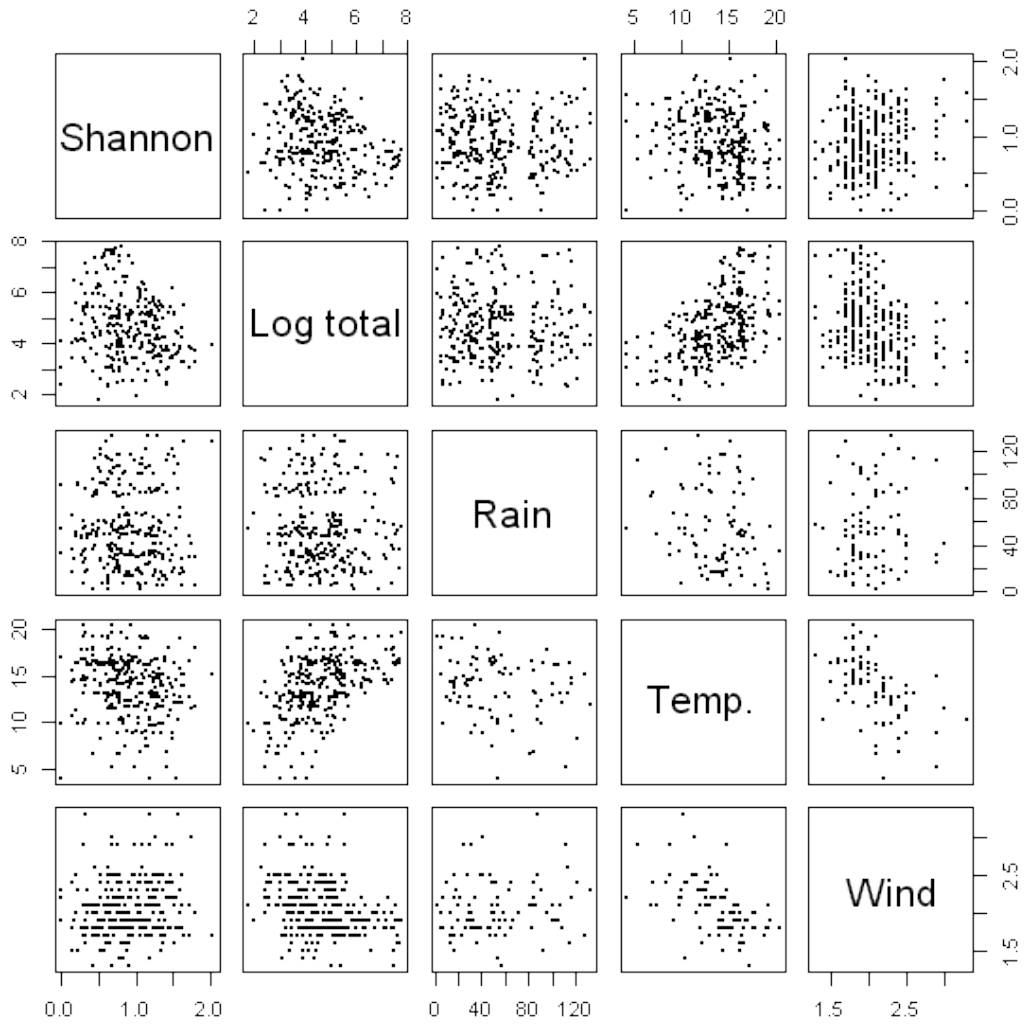

Figure 3.11: Scatterplots of the Rothamsted Transect-Month responses and rain, temperature and wind covariates. There are three transects and thus three response values for each value of rain, temperature and wind.

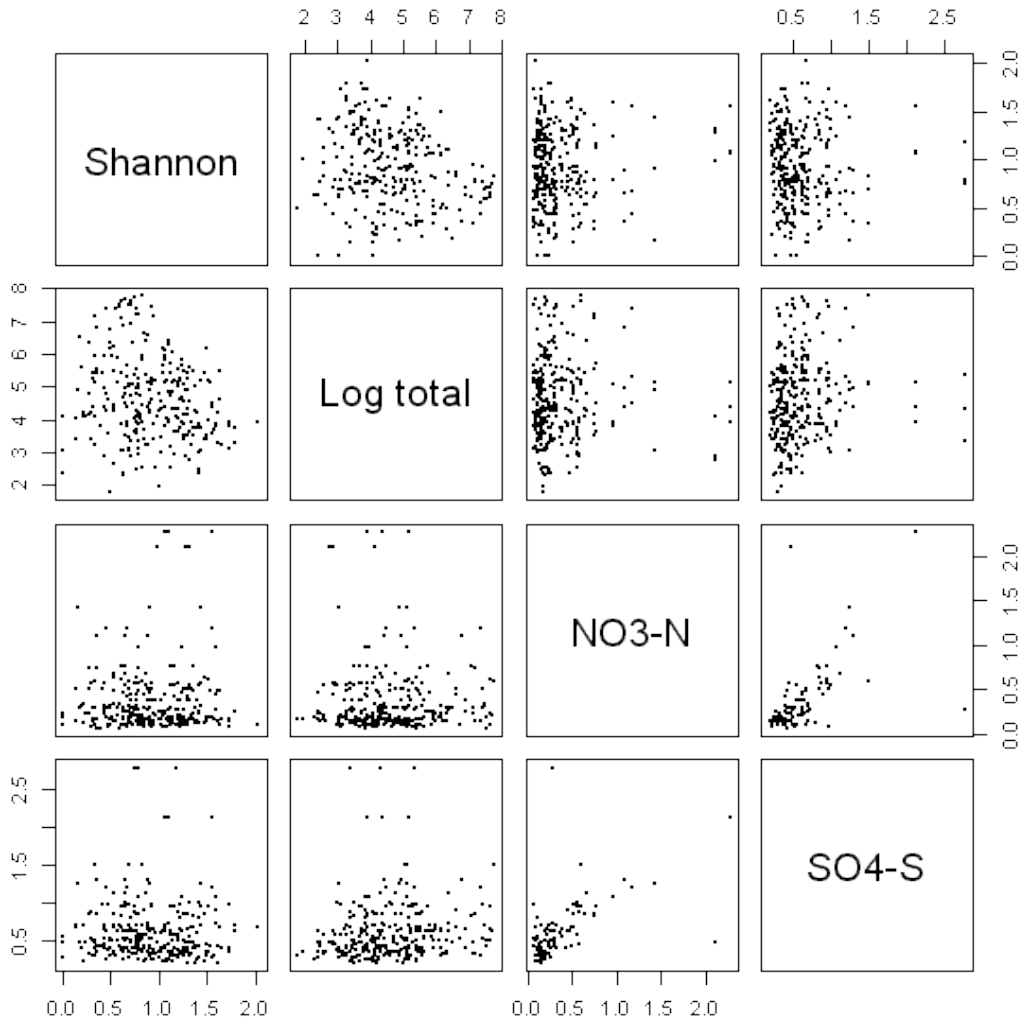

Figure 3.12: Scatterplots of the Rothamsted Transect-Month responses and Nitrate-Nitrogen and Sulphate-Sulphur covariates. There are three transects and thus three response values for each value of nitrogen and sulphur deposition.

Model selection

As in the previous chapter, selection of the covariates in the linear mixed models in this chapter will be conducted by backward selection, based on the AICc value of the proposed model. As in the fitting of GLMMs in chapter 2, the models will be fitted first using Maximum Likelihood (ML). The final chosen model for each site and response value will be refitted using Restricted Maximum Likelihood (REML). The initial model for the selection process is:

$$I_{ijl} = \beta_1 R_{ij} + \beta_2 T_{ij} + \beta_3 W_{ij} + \beta_4 N_{ij} + \beta_5 S_{ij} + \beta_6 Y_i + \beta_{7j} M_j + Z_i \mathbf{b}_i + Z_l \mathbf{b}_l + Z_{il} b_{il} + e_{ijl} \quad (3.7)$$

In the above equation I_{ijl} is the response value for year i and month j and transect l, either as the Shannon index or log total of the beetles caught in each transect and month. The covariates are denoted as R (Rain), T (Temperature), W (Wind), N (Nitrate as Nitrate-Nitrogen), S Sulphate as Sulphate Sulphur, Y (Year) and M (Month), with coefficients denoted as $\beta_1, \ldots, \beta_6, \beta_{7,5}, \ldots, \beta_{7,11}$ and the error term e_{ijl}. All covariates are treated as linear, except for Month, which is treated as categorical. The seasonal trend is assumed to be constant across years, so there is no interaction term between Month and Year.

Habitat is not included as an explanatory covariate, due to the fact that variation between transects is accounted for by the random effect of Transect. The random effects coefficients $\mathbf{b}_i \sim N\left(0, \sigma_1^2\right)$, $\mathbf{b}_l \sim N\left(0, \sigma_2^2\right)$ and $b_{il} \sim N\left(0, \sigma_3^2\right)$. As in the models in table 3.5, an AR(1) model is fitted to estimate the correlation between consecutive residual errors. No interaction terms are fitted, in favour of a simpler, more understandable model structure. This means that if interactions between covariates are present, they will not be detected, as backward selection is used, with the initial model as in equation 3.7. The selection process is by the criterion of the AICc value, as in chapter 2.

The null model for the Rothamsted transect data is considered to have the same random effects structure as the model in equation 3.5, with Year and Transect nested within Year. No fixed effects apart from the intercept are fitted, in order that space and time covariates, e.g. a linear trend of Year or a categorical Month factor, do not preclude environmental covariates from being fitted, if they may be more appropriate in the final selected model. The results of this process for the Rothamsted transect data are shown in table 3.6.

Model	Covariates	AICc	Dev. expl.
1	R + T + W + N + S + Y + M	613.4	27.5%
2	R + T + N + S + Y + M	611.2	27.5%
3	R + T + N + S + M	609.1	27.5%
4	T + N + S + M	607.5	27.4%
5	T + N + M	605.8	27.4%
6	**N + M**	**605.3**	**27.1%**
7	N	808.4	0.1%
8	M	606.9	26.7%

Table (a)

Model	Covariates	AICc	Dev. expl.
1	R + T + W + N + S + Y + M	173.7	29.9%
2	T + W + N + S + Y + M	171.4	29.9%
3	T + N + S + Y + M	169.1	29.9%
4	T + N + Y + M	167.1	29.7%
5	**T + N + M**	**166.7**	**29.7%**
6	N + M	168.4	26.8%
7	T + M	169.4	26.3%
8	T + N	198.1	6.2%

Table (b)

Table 3.6: Selection process of the models for the Rothamsted Transect-Month data. Table (a) shows the log total response model, where the chosen model is number 6; the chosen Shannon index model in table (b) is number 5. Both are indicated by bold type. The deviance explained is calculated relative to the respective null model for each response with an intercept as the sole fixed effect. The random effects in the null model are as in equation 3.7: Year, Transect and Transect nested within Year. The covariates are denoted as follows: R = Rain, T = Temperature, W = Wind, N = Nitrogen deposition, S = Sulphur deposition, Y = Year, M = Month.

	Log total			Shannon index		
Covariate	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Temp °C	-	-	-	0.02	0.01	0.03
NO3-N (mg l^{-1})	−0.24	0.13	0.06	0.13	0.06	0.05
Month 5	4.19	0.54	0.01	0.63	0.22	0.01
Month 6	5.02	0.54	0.01	0.55	0.26	0.04
Month 7	5.18	0.54	0.01	0.19	0.29	0.50
Month 8	6.04	0.54	0.01	0.15	0.29	0.61
Month 9	5.71	0.54	0.01	0.45	0.25	0.08
Month 10	3.92	0.54	0.02	0.65	0.20	0.01
Month 11	3.33	0.55	0.02	0.62	0.18	0.01

Random effects	Log total	Shannon index
Year (σ_1)	$< 1 \times 10^{-4}$	0.04
Transect (σ_2)	0.91	0.20
Transect within Year (σ^3)	0.14	0.20
Residual	0.68	0.28
AR(1) ϕ est.	0.09	0.05

Table 3.7: Selected Rothamsted site Transect-Month models.

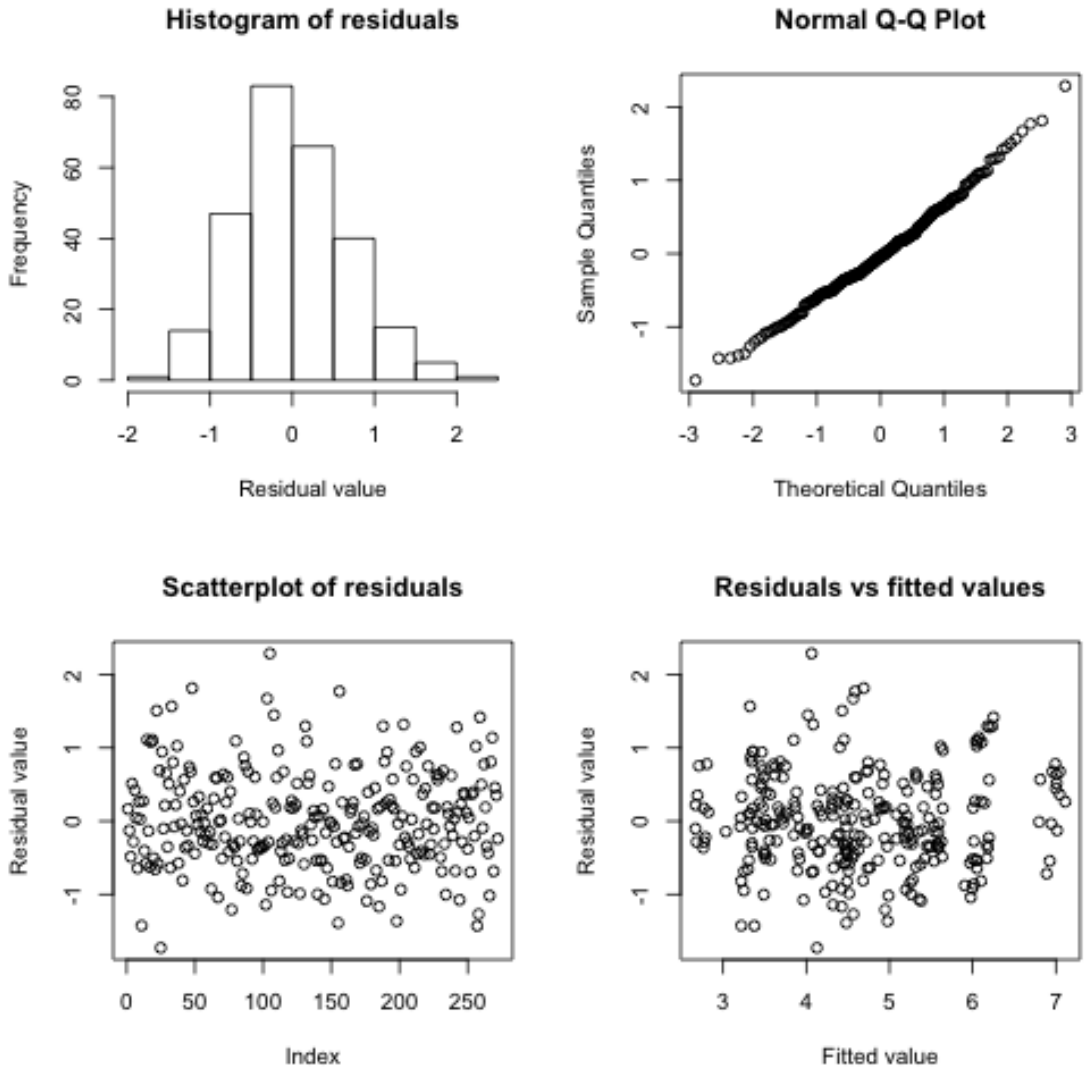

Figure 3.13: Diagnostic plots of the chosen Rothamsted log total model in table 3.7.

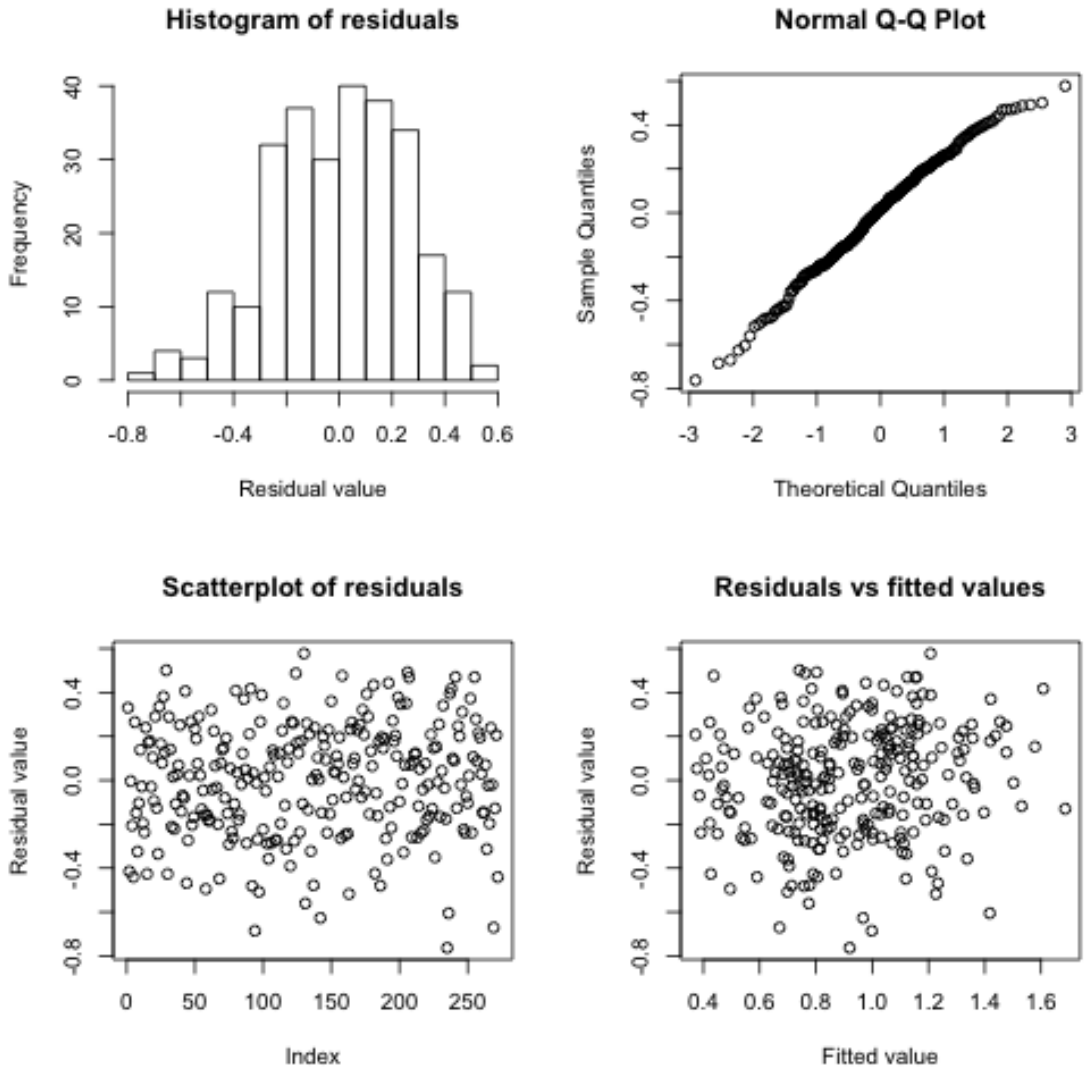

Figure 3.14: Diagnostic plots of the chosen Rothamsted Shannon index model; the parameter estimates are shown in table 3.7.

The selected final models for the Rothamsted Transect-Month data are displayed in table 3.7. Month is also included in both final models, with effects similar to those in table 3.5. Nitrate-Nitrogen deposition is estimated to have a negative effect in the log total model and a positive effect in the Shannon model. Temperature is present in the Shannon index model with a slight positive coefficient of 0.02.

In the Shannon index model, the slight positive Temperature and Nitrate-Nitrogen coefficients indicate an increase in the index value at greater temperatures and Nitrate-Nitrogen

levels respectively. The reason for these opposite effects in the two models may be as follows: If a few dominant genera are affected by higher temperatures and Nitrate-Nitrogen levels such that their activity density is lowered, the log total of beetles caught in a given transect would fall while the Shannon index would rise.

In comparison with the models in table 3.5, there is very little change in the random effect standard deviations. The correlation ϕ estimate in the AR(1) structure shows little change from the starting decomposition with estimates of 0.09 and 0.05 in the respective log total and Shannon models, indicating very little residual correlation between the Transect-Month responses. The reduction in the deviance explained in the final models compared with the 'null' models is nearly 30% for the Shannon index model and just under 27% for the log total response. There is therefore still a large amount of variability left unaccounted for in the responses. The within Month, between Transect variability estimated in the preliminary model in table 3.4 cannot be explained by the covariate information. Given the environmental covariate data is available at one position at each site, variability between transects for a given timepoint cannot be fully explained by covariate values which do not vary across the site. The diagnostic plots in figures 3.13 and 3.14 give no cause for inferring that the model assumptions have been violated.

3.4.2 Sourhope

Sourhope, in contrast with Rothamsted, is at a remote upland location in the Scottish Borders. Two of the transects are positioned in moorland and the other in grassland. The time series for the Sourhope Shannon index values for each transect are shown in figures 3.15, 3.16 and 3.17. The trend for these transects is somewhat different to those witnessed in the transects at Rothamsted. There is a strong seasonal trend in the two moor transects with a peak in the Shannon index in the middle of the sampling season; a less discernible effect is seen in the grass transect. Long-term trends suggest a slight increase in the grass transect and decreases in the moor transects, particularly with respect to later sampling seasons.

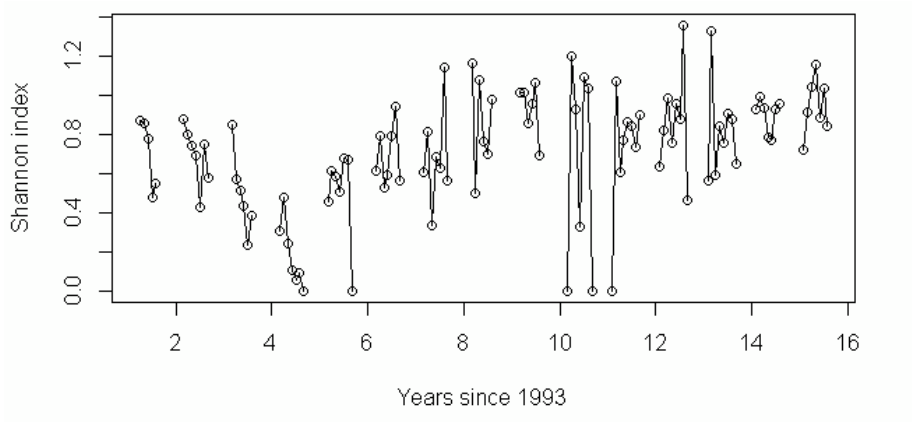

Figure 3.15: Time series of monthly Shannon index values for the grass transect at Sourhope.

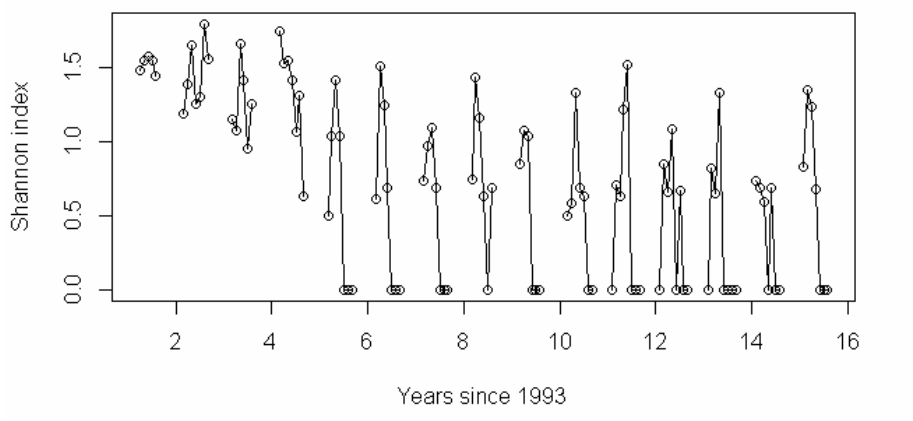

Figure 3.16: Time series of Monthly Shannon index values for the first moor transect at Sourhope.

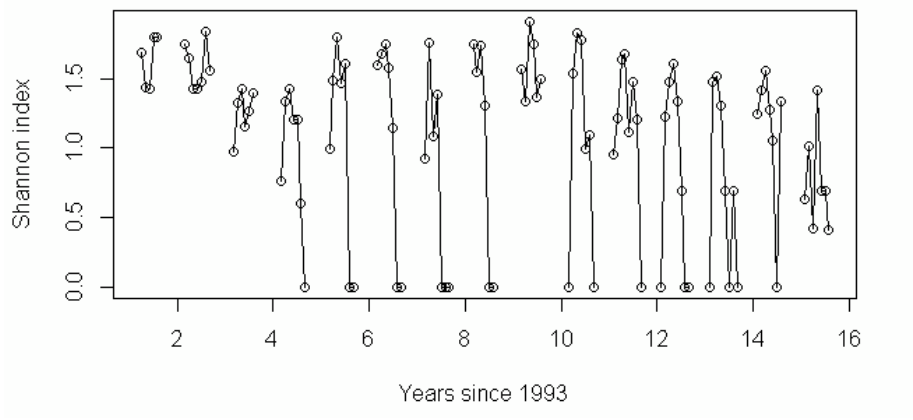

Figure 3.17: Time series of Monthly Shannon index values for the second moor transect at Sourhope.

As in the Rothamsted, exploratory models of the beetle responses are fitted for Sourhope for the log total and Shannon index. The results are shown in table 3.8. Given the relatively small number of beetles caught at Sourhope in comparison to Rothamsted, the responses of log total and Shannon index are more strongly correlated and peaks in both responses are seen Month 6: June. These similar trends indicate that there is not the same dominance of a few genera at Sourhope as at Rothamsted. Thus the increase of a single genus lowers the Shannon index when they are caught in abundance. There is a significant negative effect of year in both models, suggesting that both indices are decreasing overall over the years of survey. The estimated random effect standard deviations for Transect in both models show that the variability within transects is much greater than between the transects. The correlation parameter estimates of ϕ are 0.37 and 0.23 for the log total and Shannon index responses respectively. These estimates are reasonably large in comparison with the Rothamsted models in table 3.5, but do not indicate high correlation using the autoregression function with lag 1.

	Log total			Shannon index		
Covariate	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Year	-0.10	0.03	0.01	-0.03	0.01	0.01
Month 4	2.68	0.60	<0.01	0.88	0.19	<0.01
Month 5	3.94	0.54	<0.01	1.20	0.15	<0.01
Month 6	4.34	0.54	<0.01	1.33	0.15	<0.01
Month 7	4.24	0.54	<0.01	1.39	0.15	<0.01
Month 8	3.88	0.54	<0.01	1.13	0.15	<0.01
Month 9	3.40	0.54	<0.01	0.89	0.15	<0.01
Month 10	2.99	0.54	0.01	0.90	0.15	<0.01
Month 11	1.96	0.55	0.02	0.52	0.16	0.01

Random effects	Log total	Shannon index
Year (σ_1)	0.39	$< 1 \times 10^{-4}$
Transect (σ_2)	0.77	0.18
Transect within Year (σ_3)	0.38	0.24
Residual	0.89	0.39
AR(1) ϕ est.	0.37	0.23

Table 3.8: Starting decomposition of the Sourhope Transect-Month GLMMs.

The same process of model selection is carried out for the Sourhope transects as for the Rothamsted data in equation 3.7. The same covariates are tested: Rain, Temperature, Windspeed, Nitrate-nitrogen, Sulphate-sulphur, Year and Month.

Model	Covariates	AICc	Dev. expl.
1	R + T + W + N + S + Y + M	831.2	16.3%
2	T + W + N + S + Y + M	829.3	16.3%
3	**T + N + S + Y + M**	**827.1**	**16.3%**
4	N + S + Y + M	828.9	15.9%
5	T + S + Y + M	829.3	15.9%
6	T + N + Y + M	828.7	15.9%
7	T + N + S + M	835.1	15.2%
8	T + N + S + Y	879.8	8.9%

Table (a)

Model	Covariates	AICc	Dev. expl.
1	R + T + W + N + S + Y + M	354.0	27.0%
2	T + W + N + S + Y + M	352.0	26.8%
3	T + N + S + Y + M	349.9	26.8%
4	T + S + Y + M	349.7	26.3%
5	**T + Y + M**	**347.6**	**26.3%**
6	Y + M	348.2	25.7%
7	T + M	353.0	24.5%
8	T + Y	391.3	12.2%

Table (b)

Table 3.9: Selection process of the GLMMs for the Sourhope Transect-Month data. Table (a) shows the log total response model, where the chosen model is number 3; the chosen Shannon index model in table (b) is number 5. The deviance explained has been tested against the same null model structure as the Rothamsted models in table 3.6, with an intercept as the sole fixed effect and random effects of Year and Transect nested within Year as in equation 3.7. The covariates are denoted as follows: R = Rain, T = Temperature, W = Wind, N = Nitrogen deposition, S = Sulphur deposition, Y = Year, M = Month.

	Log total			Shannon index		
Covariate	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Temp °C	0.10	0.05	0.05	0.04	0.02	0.10
NO3-N (mg l^{-1})	0.62	0.29	0.03	-	-	-
SO4-S (mg l^{-1})	-0.67	0.34	0.05	-	-	-
Year	-0.10	0.03	<0.01	-0.03	0.01	0.01
Month 4	2.18	0.66	0.01	0.68	0.22	<0.01
Month 5	3.20	0.69	<0.01	0.90	0.24	<0.01
Month 6	3.31	0.77	<0.01	0.94	0.28	<0.01
Month 7	3.02	0.86	<0.01	0.92	0.33	0.01
Month 8	2.67	0.86	<0.01	0.67	0.32	0.04
Month 9	2.36	0.78	0.01	0.50	0.28	0.01
Month 10	2.31	0.67	0.01	0.61	0.23	0.01
Month 11	1.46	0.61	0.01	0.34	0.19	0.09

Random effects	Log total	Shannon index
Year (σ_1)	0.34	$< 1 \times 10^{-4}$
Transect (σ_2)	0.77	0.18
Transect within Year (σ_3)	0.38	0.24
Residual	0.89	0.38
AR(1) ϕ est.	0.36	0.23

Table 3.10: Selected final Sourhope site Transect-Month models.

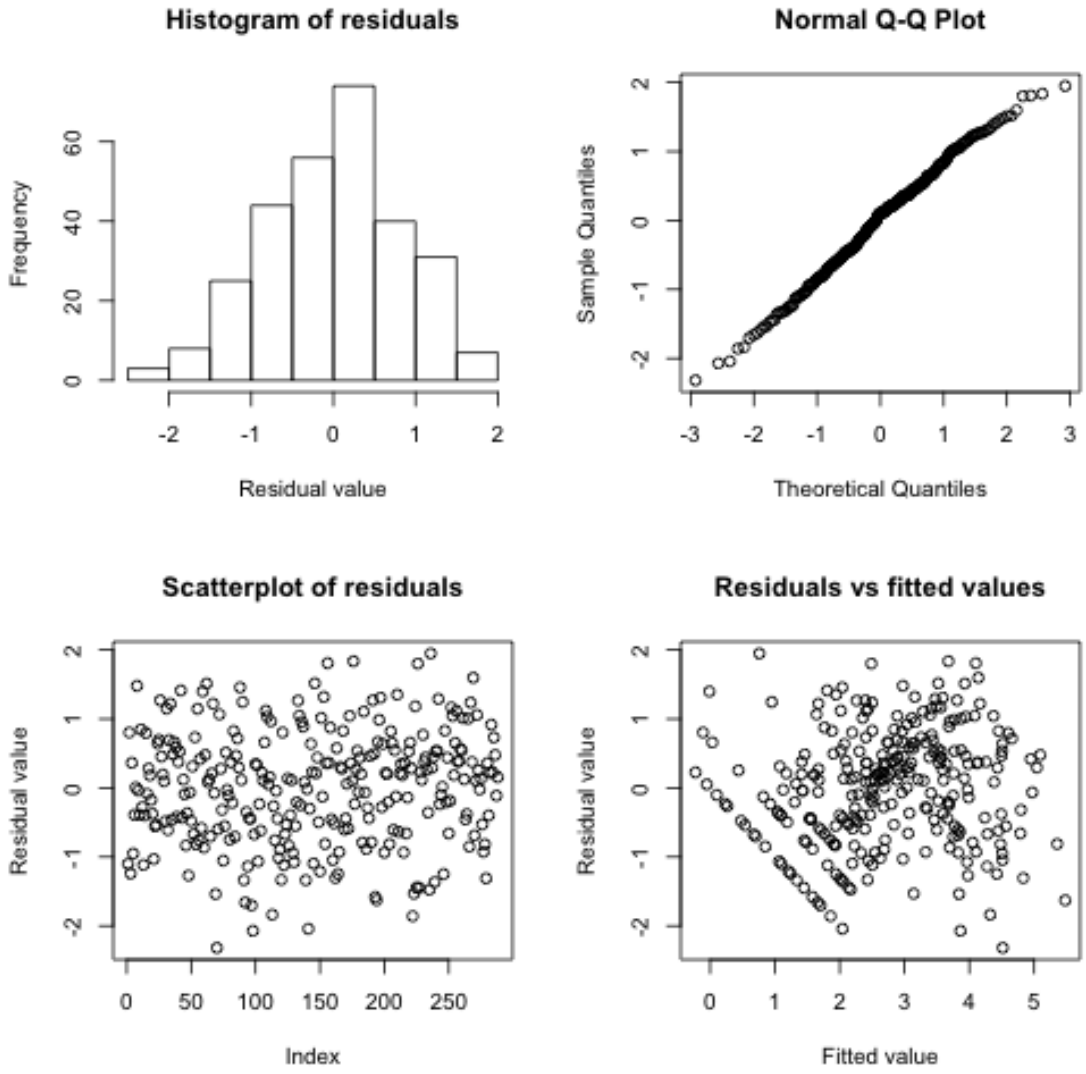

Figure 3.18: Diagnostic plots of the chosen Sourhope log total model; the parameter estimates are shown in table 3.10.

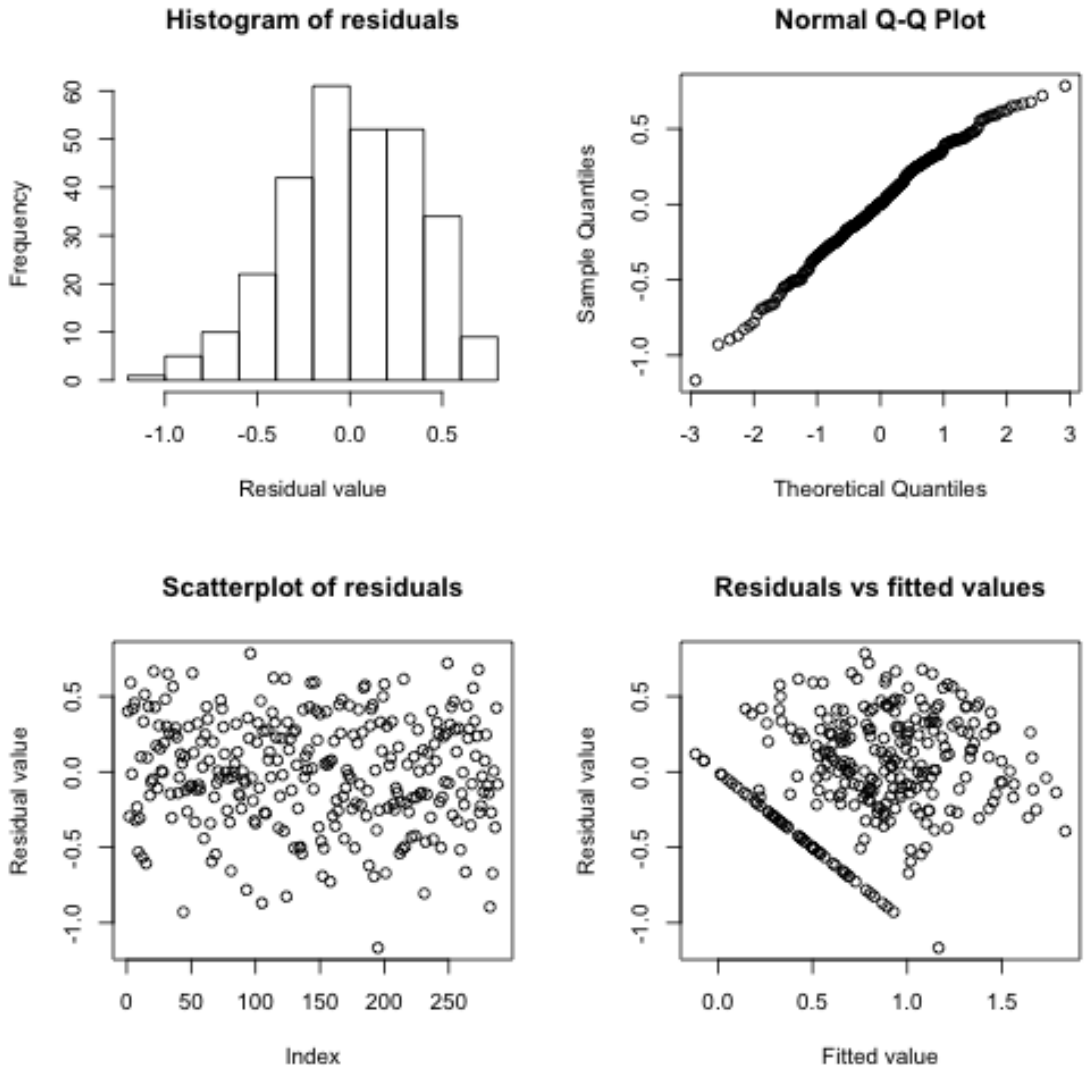

Figure 3.19: Diagnostic plots of the chosen Sourhope Shannon index model; the parameter estimates are shown in table 3.10.

The selection process and final models chosen by AICc criterion for the Sourhope models are shown in tables 3.9 and 3.10. The same effects selected for both responses in the final models are Temperature, Year and Month. Temperature has a small positive coefficient of 0.10 in the log total model and 0.04 in the Shannon model. This is a positive effect of temperature In addition to the seasonal trend explained by Month. Nitrate-nitrogen and Sulphate-sulphur are both present in the log total model, with positive and negative coefficients estimated respectively.

The parameter estimates for the Year and Month covariates are similar to those in the starting decompositions, as are the estimated random effects and autoregression structure, as in the Rothamsted model. This again indicates that the environmental covariates present in the final model do not explain much extra variation in the model responses. The diagnostic plots in figures 3.18 and 3.19 give no real cause for concern that the model assumptions have been violated. Due to the low response values in the Sourhope transects, straight lines appear in the lower-right image of the model diagnostics, showing a negative relationship between some fitted and residual values. This is due to the high number of responses that have a particular log total or Shannon index value. The deviance explained in the final models in table 3.9 are not as high as the Rothamsted models; there is approximately 16% explained in the log total model and just about 26% in the Shannon index model. Given the complex model selected for the log total response, the low deviance explained indicates there is a large amount of variability in the beetle population which is not accommodated for by these covariates.

3.5 Multi-site models

The Shannon index responses at all ten sites in the analysis are shown in a boxplot in figure 3.20. Rothamsted has a slightly smaller interquartile range and marginally larger median value than Sourhope. All sites have responses of zero within the period of survey, although the number of such records is usually small and they are normally only at the beginning or end of the sampling season. Moor House has the smallest median, with a high number of responses equal to zero; in comparison North Wyke has the largest median and very few zero responses.

The scatterplots of the explanatory covariates and model responses are shown in figures 3.21 and 3.22. There appears to be a positive correlation between temperature and the log total response. There is also a slight negative correlation between log total and wind. The other variables do not appear to show clear relationships with the response.

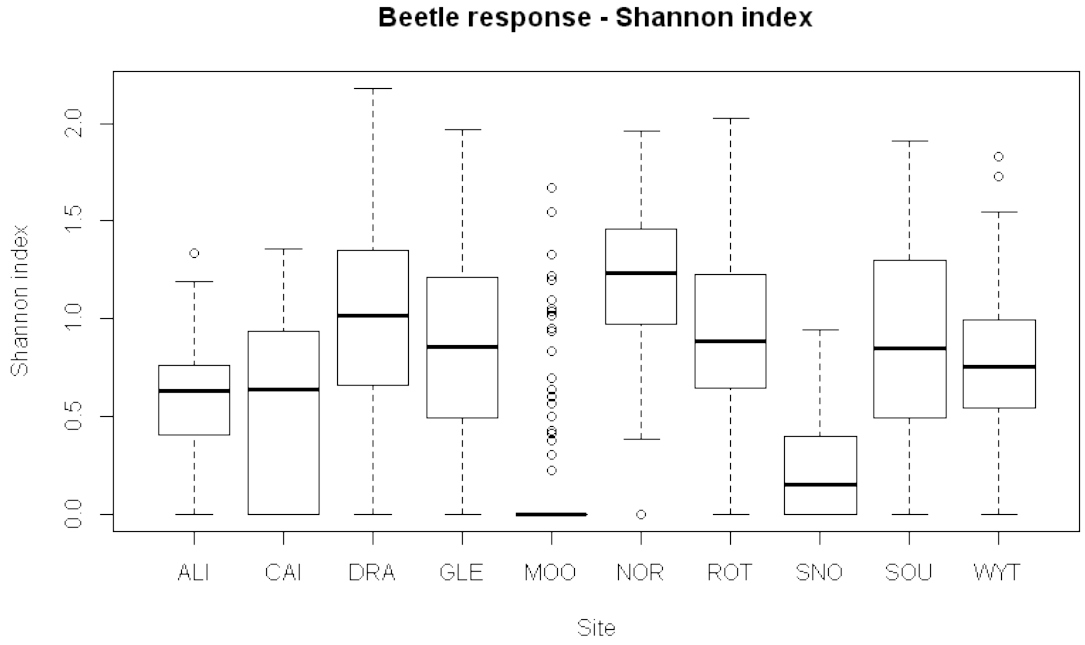

Figure 3.20: Boxplot of the transect-month Shannon index response values for all sites. Site names are: ALI - Alice Holt, CAI - Cairngorm, DRA - Drayton, GLE - Glensaugh, MOO - Moor House, NOR - North Wyke, ROT - Rothamsted, SNO - Snowdon (Yr Wyddfa), SOU - Sourhope and WYT - Wytham.

For the multi-site models, a starting decomposition is structured in a similar way to the single site models:

$$I_{ijkl} = \beta_1 Y_i + \beta_{2j} M_j + Z_i \mathbf{b}_i + Z_k \mathbf{b}_k + Z_{kl} \mathbf{b}_{kl} + Z_{ik} \mathbf{b}_{ik} + Z_{ikl} b_{ikl} + e_{ijkl} \tag{3.8}$$

where the response I_{ijkl} is calculated for the ith year, jth month kth site and and lth transect. Month (M) is included as a categorical factor and Year (Y) as continuous. In expanding the single-site model structure, Year and Site are included as main random effects, with Transect nested within Site also. These terms are denoted by the matrices $\mathbf{Z}_i$, $\mathbf{Z}_k$, $\mathbf{Z}_{kl}$ $\mathbf{Z}_{ik}$ and $\mathbf{Z}_{ikl}$. The associated vectors of coefficients $\mathbf{b}_i$, $\mathbf{b}_k$, $\mathbf{b}_{ik}$, $\mathbf{b}_{kl}$ and $\mathbf{b}_{ikl}$ are estimates of the variation between Years, between Sites, Transects within Sites, Sites within Years and Transects within Sites and Years. The coefficients are distributed as $\mathbf{b}_i \sim N\left(0, \sigma_1^2\right)$, $\mathbf{b}_k \sim N\left(0, \sigma_1^2\right)$, $\mathbf{b}_{kl} \sim N\left(0, \sigma_1^3\right)$, $\mathbf{b}_{ik} \sim N\left(0, \sigma_2^4\right)$, $b_{ikl} \sim N\left(0, \sigma_5^2\right)$.

An AR(1) model is again fitted to estimate the correlation between the residual errors e_{ijkl} within each Transect, Site and Year. The error term e_{ijkl} in Year i Site k and transect l in Month j is fitted in the correlation structure as:

$$e_{ijkl} = \phi e_{i,j-i,kl} + q_{ijkl} \tag{3.9}$$

where $e_{i,j-1,kl}$ is the residual value at Year i and Month $j-1$, in a defined site k and transect l, ϕ is a constant where $-1 < \phi < 1$ and q_{ijkl} is a random process, normally distributed with mean 0 and variance σ_Q^2. The estimated value of ϕ is the correlation reported in table 3.5. The starting decomposition models for the multi-site data are displayed in table 3.11.

The starting decomposition shows Year to have a very significant albeit slight negative effect in both models (Table 3.11). The largest Month parameters are in month 7 and 8 for the log total response, and months 5 and 6 for the Shannon index. The random effects standard deviations show that the variation between Years in both models, estimated by the standard deviation σ_1 is much smaller than that both the variation between Sites within Years, or between Transects within Sites and Years, estimated by σ_1 and σ_2 respectively. For both models, the Site random effect standard deviation is the largest and Transect, which is nested within Site, is smaller than the respective residual effect. It can be inferred that the largest variability is between sites, whereas the residual standard deviation is estimated to be more than twice the standard deviation between Transects. This indicates there is considerable variability which cannot be explained by the site environmental covariates. The estimate of the correlation parameter ϕ is much larger for the log total is similar to the estimate of ϕ in the initial model of Site-Year aggregated responses in table 3.2. The Shannon index ϕ is much smaller, indicating a relatively lower temporal correlation than in the log total model.

	Log total			Shannon index		
Covariate	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Year	−0.04	0.01	<0.01	−0.01	<0.01	<0.01
Month 3	1.47	0.54	0.02	−0.03	0.24	0.89
Month 4	2.09	0.25	<0.01	0.80	0.12	<0.01
Month 5	3.32	0.23	<0.01	0.94	0.11	<0.01
Month 6	3.96	0.23	<0.01	0.97	0.11	<0.01
Month 7	4.00	0.23	<0.01	0.89	0.11	0.01
Month 8	3.91	0.23	<0.01	0.78	0.11	<0.01
Month 9	3.30	0.23	<0.01	0.80	0.11	<0.01
Month 10	2.93	0.23	<0.01	0.75	0.11	<0.01
Month 11	1.81	0.23	<0.01	0.45	0.11	<0.01
Month 12	0.98	0.36	0.05	0.15	0.16	0.36

Random effects	Log total	Shannon index
Year (σ_1)	$< 1 \times 10^{-4}$	0.03
Site (σ_2)	1.09	0.33
Transect within Site (σ_3)	0.66	0.13
Site within Year (σ_4)	0.50	0.12
Transect within Site within Year (σ_5)	0.21	0.11
Residual	0.81	0.34
AR(1) ϕ est.	0.25	0.12

Table 3.11: Starting decomposition of the multi-site Transect-Month GLMMs.

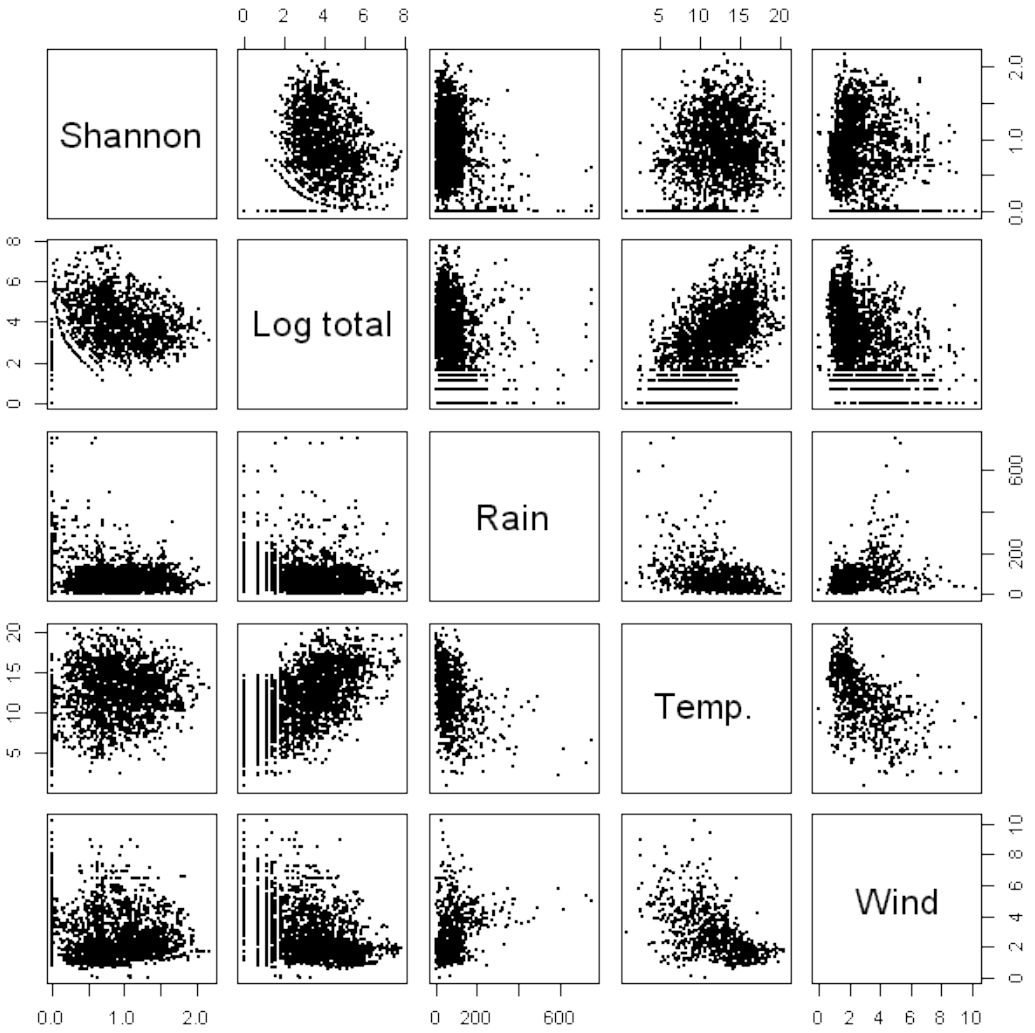

Figure 3.21: Scatterplots of the Rothamsted Transect-Month responses and rain, temperature and wind covariates for all ten sites.

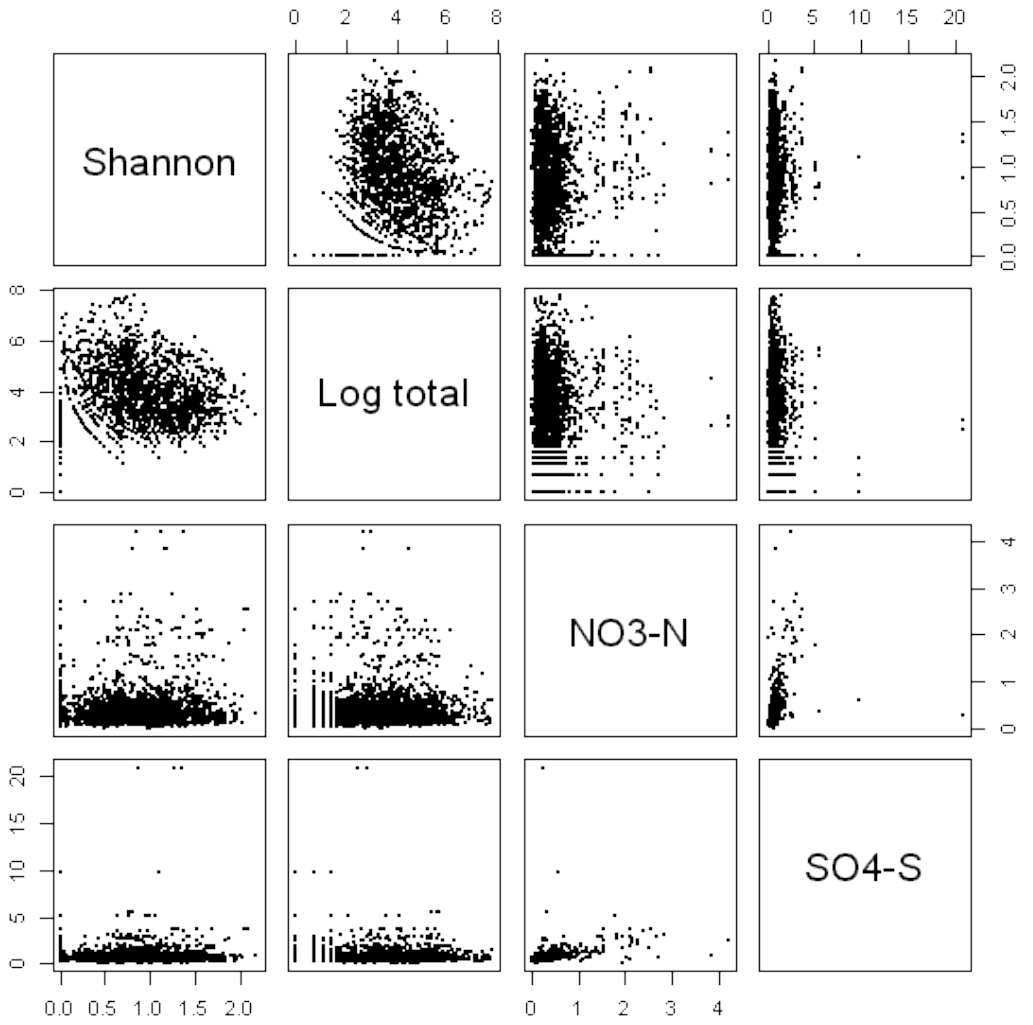

Figure 3.22: Scatterplots of the Transect-Month responses and Nitrate-Nitrogen and Sulphate-Sulphur covariates for all ten sites.

The same environmental covariates will be used in the multi-site model, as in the Rothamsted and Sourhope models. The initial model for the selection process for the multi-site model is:

$$I_{ijkl} = \beta_1 R_{ijk} + \beta_2 T_{ijk} + \beta_3 W_{ijk} + \beta_4 N_{ijk} + \beta_5 S_{ijk} + \beta_6 Y_i + \beta_{7j} M_j + Z_i \mathbf{b}_i + Z_k \mathbf{b}_k + Z_{kl} \mathbf{b}_{kl} + Z_{ik} \mathbf{b}_{ik} + Z_{ikl} b_{ikl} + e_{ijkl} \quad (3.10)$$

In the above equation I_{ijkl} is the response value for year i and month j in site k and transect l. The covariates are denoted as R (Rain), T (Temperature), W (Wind), N (Nitrate as Nitrate-Nitrogen), S (Sulphate as Sulphate Sulphur,) Y (Year) and M (Month). All covariates are treated as linear, except for Month, which is treated as categorical. The random effects are fitted as Year, Site nested within Year and Transect nested within Site and Year, as in equation 3.8. An AR(1) process is also fitted as in equation 3.9. The selection process by AICc criterion for the multi-site models is shown in tables 3.12.

Model	Covariates	AICc	Dev. expl.
1	R + T + W + N + S + Y + M	6227.8	16.5%
2	R + T + W + N + Y + M	6225.8	16.5%
3	T + W + N + Y + M	6223.8	16.5%
4	**T + N + Y + M**	**6221.8**	**16.5%**
5	N + Y + M	6231.1	16.3%
6	T + Y + M	6222.0	16.5%
7	T + N + M	6230.7	16.3%
8	T + N + Y	6485.3	12.7%

Table (a)

Model	Covariates	AICc	Dev. expl.
1	R + T + W + N + S + Y + M	2063.7	17.2%
2	R + T + W + N + Y + M	2063.2	17.2%
3	T + W + N + Y + M	2063.0	17.1%
4	T + W + Y + M	2062.7	17.0%
5	**W + Y + M**	**2060.8**	**17.0%**
6	Y + M	2080.7	16.1%
7	W + M	2066.9.0	16.7%
8	W + Y	2409.7	1.9%

Table (b)

Table 3.12: Selection process of the GLMMs for the multi-site Transect-Month data. Table (a) shows the log total response model, where the chosen model is number 4; the chosen Shannon index model in table (b) is number 5. Both chosen models are in bold type. The percentage of deviance explained is calculated in relation to the 'null' model, with a sole intercept as a fixed effect and the random effects unchanged, as in in equation 3.10. The covariates are denoted as follows: R = Rain, T = Temperature, W = Wind, N = Nitrogen deposition, S = Sulphur deposition, Y = Year, M = Month.

The selected final models for the multi-site Transect-Month data are displayed in table 3.13. There is a small positive effect for Temperature and a small negative effect for Nitrate-Nitrogen in the log total model: the respective estimated coefficients are 0.05 and -0.08. The positive temperature coefficient for log total concurs with the scatterplot observed in figure 3.21. The Nitrate-nitrogen relationship concurs with the Rothamsted log total model, which also showed a negative trend. For the Shannon index response, the chosen covariates include a small negative effect for Wind (Table 3.13). The environmental covariate trends are marginal in relation to the seasonal trend explained by the Month covariate.

The relationships found in the multi-site models could be the result of trends across time at all sites, where, for instance, an increase in temperature is correlated with an increase in the beetle response. Temperature was also included in three of the four Rothamsted and Sourhope models, where no spatial information on temperature was available. This relationship could also be based upon the spatial correlation between the beetle response and the fitted covariate. Given the random effect of Year has a very small estimated deviation, (σ_1), for both models in table 3.13, it is inferred that these relationships are based upon the latter possibility, by explaining variability between sites rather than across years at all sites. The standard deviation for the random effects in the final models in table 3.13 are very similar to those in the exploratory models in table 3.11, with a slight reduction in the variation within Sites. This suggests that the environmental covariates explain some of the inter-site differences. The other random effects are very similar to the decomposition models in table 3.11.

	Log total			Shannon index		
Covariate	Estimate	Std. error	P-value	Estimate	Std. error	P-value
Temp °C	0.05	0.02	<0.01	-	-	-
NO3-N (mgl^{-1})	-0.08	0.05	0.14	-	-	-
Wind (m/sec)	-	-	-	-0.05	0.01	<0.01
Year	-0.04	0.02	<0.01	-0.01	4×10^{-3}	0.01
Month 3	1.29	0.61	0.20	0.22	0.24	0.38
Month 4	1.76	0.38	<0.01	0.95	0.12	<0.01
Month 5	2.84	0.39	<0.01	1.09	0.11	0<0.01
Month 6	3.31	0.41	<0.01	1.10	0.10	<0.01
Month 7	3.25	0.42	<0.01	1.01	0.11	<0.01
Month 8	3.17	0.42	<0.01	0.90	0.11	<0.01
Month 9	2.71	0.40	<0.01	0.94	0.11	<0.01
Month 10	2.47	0.38	<0.01	0.90	0.11	<0.01
Month 11	1.54	0.37	<0.01	0.61	0.11	<0.01
Month 12	0.81	0.46	0.09	0.33	0.16	0.05

Random effects	Log total	Shannon index
Year (σ_1)	$< 1 \times 10^{-4}$	0.04
Site (σ_2)	1.00	0.31
Transect within Site (σ_3)	0.66	0.13
Site within Year (σ_4)	0.50	0.12
Transect within Site within Year (σ_5^2)	0.21	0.11
Residual	0.80	0.34
AR(1) ϕ est.	0.25	0.12

Table 3.13: The chosen multi-site Transect-Month GLMMs, with Log total and Shannon index responses respectively.

The covariate of Wind is included in the Shannon index model. Given the estimated coefficient is negative, this could support the theory that wind is an indicator of inclement weather. The reason for this could be due to only a few genera being mobile during periods of rainfall, which then results in a lower number of genera caught and thus a reduced Shannon index value. Given the lack of information on disturbance events at each site in this model , it is difficult to put emphasis on the effect of increased windspeed and the positive correlation with the Shannon index of the beetles caught. There may be an interaction between environmental covariates occurring, which is untested in this analysis.

The Month parameter estimates in table 3.13 are fairly similar to those in the starting decompositions (Table 3.11) as was the case for both the Rothamsted and Sourhope models. There is a peak in Month 6: June for both models, with lows in Month 3 and Month 12 respectively. The diagnostic plots do not show any signs of the model assumptions having been violated. Approximately a sixth of the residual variance in both 'null' models has been explained by the respective chosen final models. This indicates there is still a large proportion of the variability in the data unexplained by the environmental covariates in the final models.

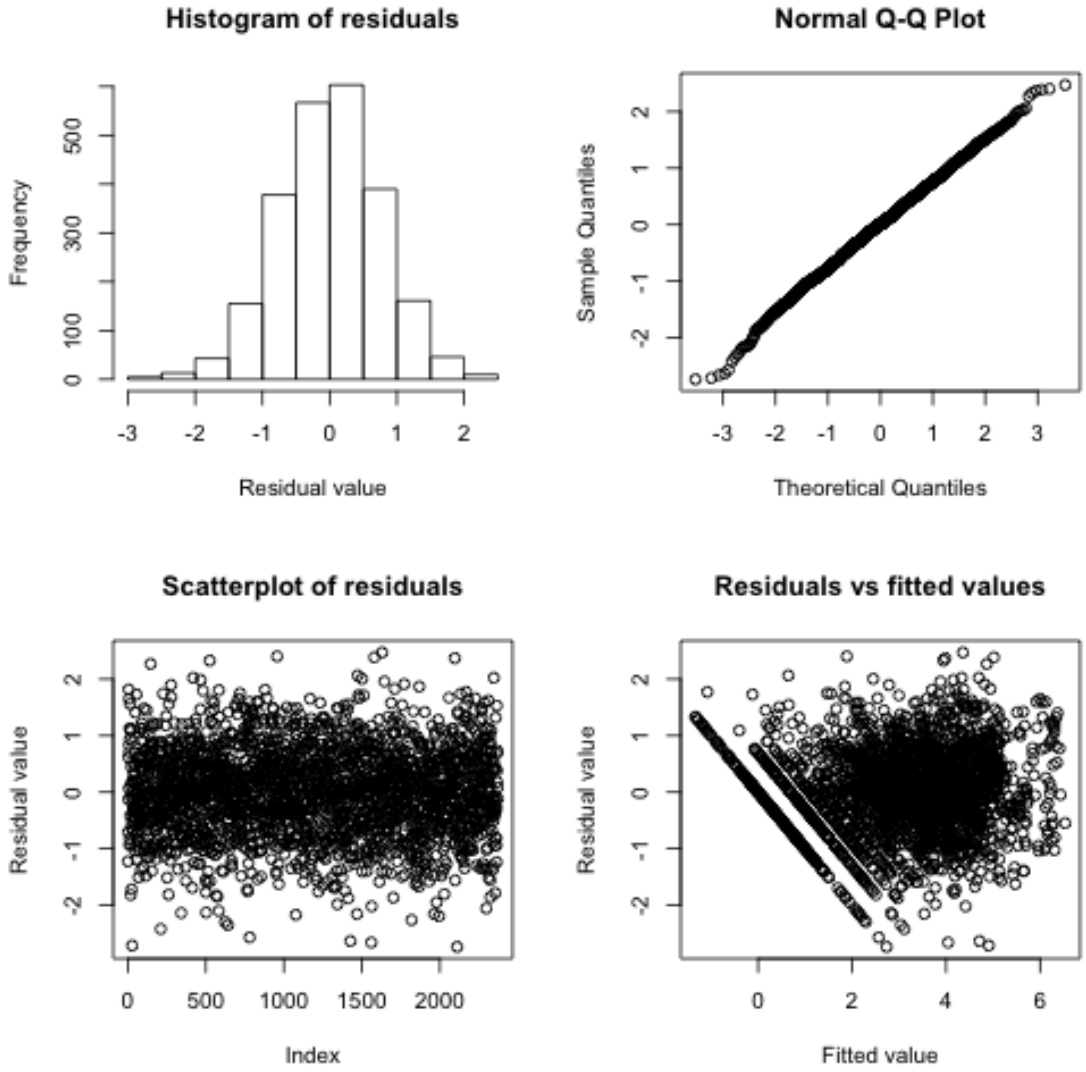

Figure 3.23: Diagnostic plots of the chosen multi-site log total GLMM; the parameter estimates are shown in table 3.13.

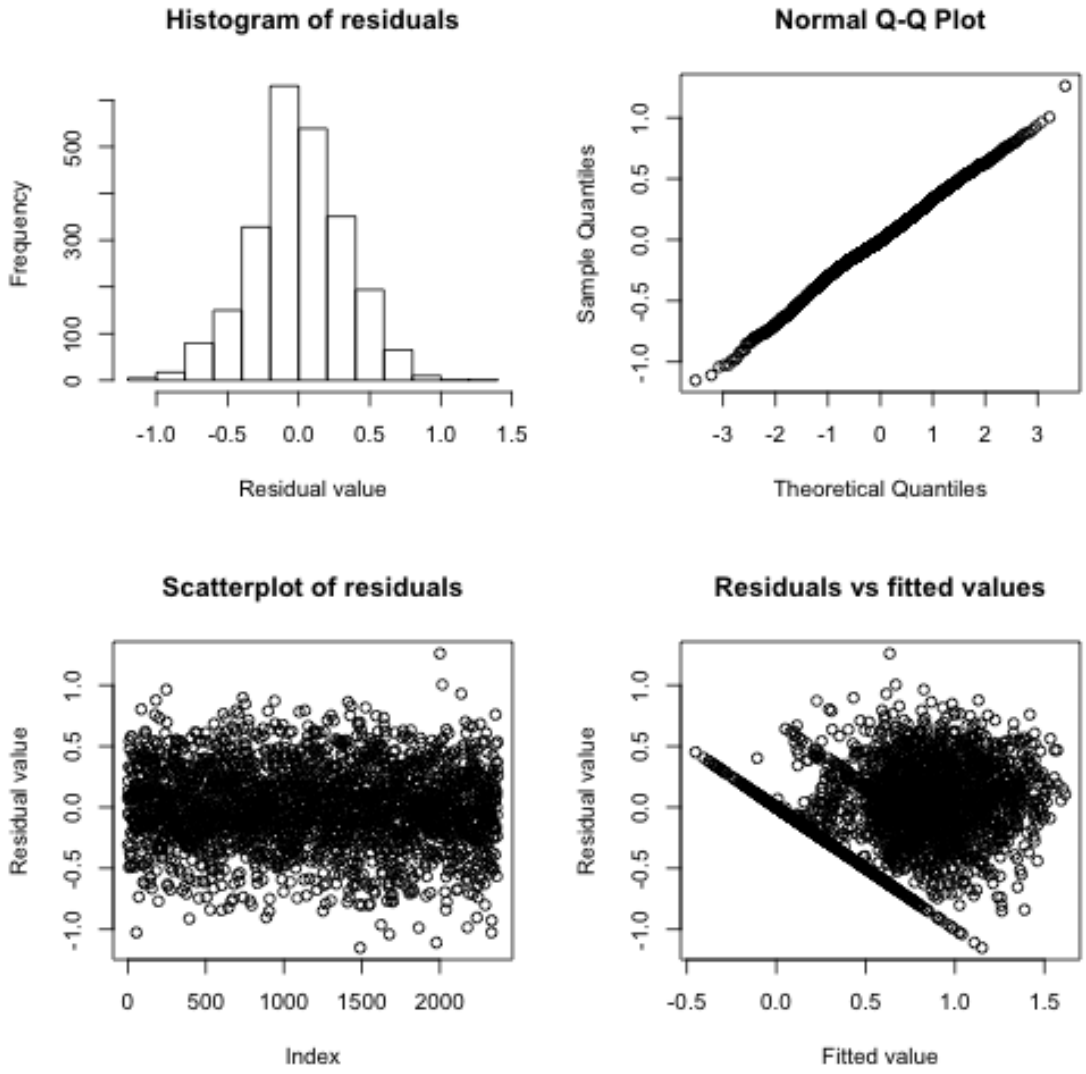

Figure 3.24: Diagnostic plots of the chosen multi-site Shannon index GLMM; the parameter estimates are shown in table 3.13.

Taking account of all covariates and sampling dates, figure 3.25 shows the fitted values for each observation from the Shannon index model in table 3.13. There are clear differences between the sites: Glensaugh, Moor House and Snowdon have the smallest fitted values; North Wyke has the largest values. The model has fitted slightly negative values at Moor House, Glensaugh and Snowdon, as this was not restricted, although technically impossible for either the log total or the Shannon index to become negative. These results, although not describing the data perfectly, follow a similar pattern to figure 3.20 depicting the response values.

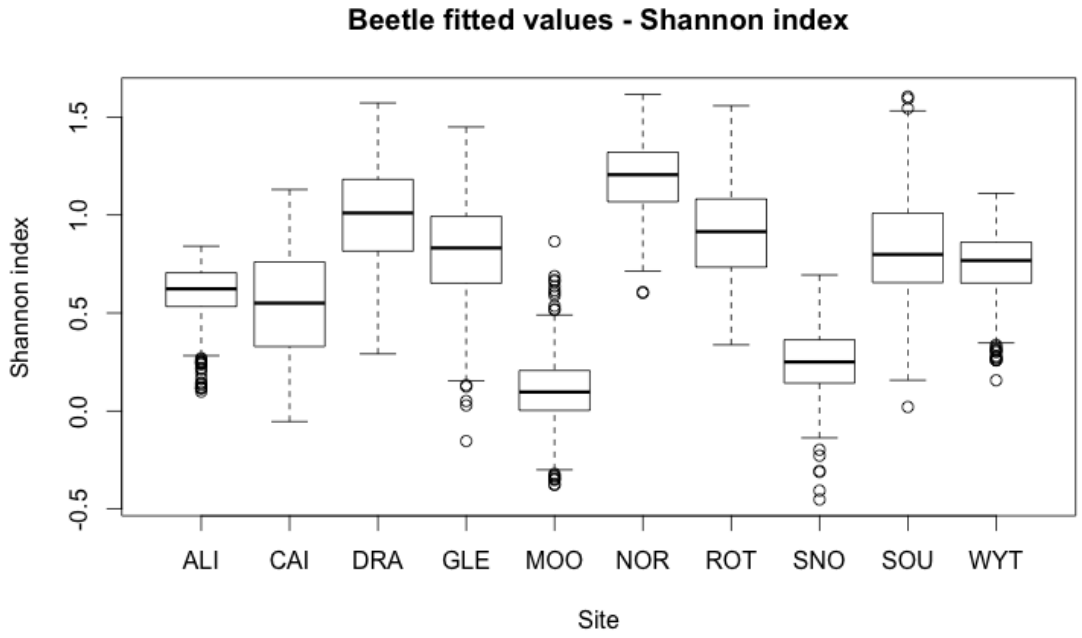

Figure 3.25: Boxplot of the transect-month Shannon index fitted values for all sites. Site names are: ALI - Alice Holt, CAI - Cairngorm, DRA - Drayton, GLE - Glensaugh, MOO - Moor House, NOR - North Wyke, ROT - Rothamsted, SNO - Snowdon (Yr Wyddfa), SOU - Sourhope and WYT - Wytham.

Due to negative fitted values obtained for three sites (Figure 3.25), a lower bounded distribution, such as the Gamma distribution may be fitted instead of the Normal in order to prevent this occurring. The difference in the single site models is indicative of differing trends obtained from this dataset, which cannot be described fully by the covariate data used.

3.6 Discussion

This chapter has focussed on linking variability in carabid communities in Great Britain with possible environmental pressures, both spatially and temporally. Two responses were selected: the log total of individuals caught and the Shannon index of the genera caught. Initial models were fitted with a Year slope for each site fitted, in order to look at the trend over time. Most of the trends were negative for both responses, two sites had significant negative trends for the log total model: Cairngorm and Moor House. A second model was

fitted with the data aggregated to the Year and Transect level within each site. Site was fitted as a random effect in this model, with an overall trend for Year fitted. Due to the repeated measures within each Year, Year was also fitted as a random effect, in order to account for the pseudoreplication. Both responses had negative trends over time; both were close to significance at the 5% level.

Linear mixed effects models were fitted for the Rothamsted, Sourhope and multi-site data in seeking to explain the variability in the beetle responses of log total and the Shannon index with the aid of environmental covariates. Two possibilities for the model structure suggested, fitting Month as a random effect or as a fixed effect. Fitting Month as a fixed effect allowed the the seasonal trend to be captured and variability within Months between Years to be explained by the other covariates. Models of all ten sites were fitted using a similar structure but with Site as a main random effect and also nested within Year. The final models for the two single sites and the multi-site models will be discussed, with reference to the chosen covariates.

Temperature was included in four of the final models for both responses at the single sites and in the multi-site models. The coefficient was estimated to be positive in all cases. The positive relationship for the multi-site log total response with temperature concurs with the study by Honek (1997), which also showed that temperature has a positive effect on the number of beetles caught in daily pitfall traps. The coefficient for nitrogen is negative for the Rothamsted log total model, but positive for the Shannon index, which contrasts with the previous studies in the literature (Raworth et al., 2004; Batáry et al., 2008). This correlation may be the result of other unobserved factors, rather than a negative effect on the beetle population.

Given that there is also a positive correlation between temperature and the Shannon index in four models, it is inferred that all genera sampled responded proportionally in relation to one another, or that rarer species showed greater activity density in response to a increase in the temperature. This could be the result of a local relationship between an increase in recorded temperatures and a decrease in the number of individuals of a dominant genus caught over the same period. This correlation with Temperature could be spurious or the specific response of a certain genus. This would mean the log total would decrease and the Shannon index would increase, if one assumed the number of other genera caught remained constant.

Similar effects were seen for the Nitrate-nitrogen covariate at Rothamsted; with opposite signs in the coefficient for the two responses tested: negative in the log total model and positive in the Shannon index model. This could be an indirect effect of higher nutrient levels in the soil, which then could result in more abundant ruderal plant species (species which can take advantage of high nutrient concentrations) and land management disturbances to cut back the foliage, which could negatively affect the number of beetles. Given that there is no information on such management practices, this relationship is difficult to infer. However, if it were the case that dominant genera were affected by such practices, this would lower the log total response and increase the Shannon index in turn. The nitrate covariate was only included in the final model for the Shannon index, which could be due to an indirect effect of higher nutrient levels which require radical pruning of the plants. The relationship is not included in the final log total model. The negative correlation of the Shannon index of beetles caught across all sites with windspeed could be due to increase in inclement weather which in turn causes a decrease in beetle movement in rarer genera and a more homogeneous catch. Alternatively, it could a be an general trend of beetle communities being dominated by only a relatively few genera in upland areas where windspeeds are higher.

At Sourhope, the effect of Temperature is positive upon the beetle response in both final models. However, there is a negative trend across the years in both models as well. The inclusion of the Year covariate indicates the reasons for this trend cannot be explained by the environmental covariates of choice, and new information on the possible pressures is necessary in order to explain this relationship. The Sourhope log total final model could be the result of spurious correlations, as it includes more covariates than the other final models and does not explain a large percentage of deviance in the response.

The Rain covariate is not included in any final models. It is considered to be a surrogate measure of soil moisture. However, given evidence that individual species have their own specific preferences for soil moisture levels, it could be that changes in the community are not observed if the log total or Shannon index are calculated. The response of the community itself could be non-linear, which would not be fitted by the GLMM structure. It could be also that the rainfall measurements at one location at each ECN site are not adequate surrogate measures of the rainfall at each transect, or even at each trap.

The estimated standard deviations of the random effects showed the variation between Transects and between Transects within Years to be larger than between Years in all final models.

The residual standard deviation is slightly larger than that between sites in the Shannon index multi-site models and slightly smaller for the log total response. This indicates there is a large amount of intra-transect variability which cannot be explained by the fitted covariates, which are only measured at the site-level. If the environmental covariates were measured beside each transect, this may allow relationships to be observed more clearly. Other covariates, such as soil moisture or habitat may explain more of the variation. Part of the variability in the beetle community could be the result of interactions within the beetle community itself, which appear as noise and do not correlate with meteorological or deposition covariates.

For the multi-site model, the standard deviation between Sites is greater than between Transect within Sites and between Years. The beetle community response of transects at the same site are inferred to more similar to each other than transects at other sites. This may be indicative of a larger-scale spatial correlation of carabid distribution across Britain. More than ten sites are necessary, in order to estimate this correlation accurately. The autoregression function of the residual errors showed estimated values of ϕ of more than 0.5 in the Sourhope multi-site log total models. The lowest values of ϕ estimated were 0.09 and 0.05 in the Rothamsted log total and Shannon index models respectively, indicating a stronger temporal correlation at the Sourhope transects. Sourhope has relatively lower log total responses than Rothamsted in the peak months of the sampling season. Therefore a higher value of ϕ does not necessarily indicate a more diverse or 'healthier' beetle community.

The final models for all sites shows more similarity with the Sourhope models than with that constructed for the Rothamsted data, given that both showed a peak in the index values near the middle of the sampling season, as opposed to a dip in the Rothamsted Shannon index model. This could be due to the beetle community response at Sourhope being more representative than at Rothamsted of the community response across all ten ECN sites of interest. Nineteen of the thirty long-term transects in the analysis are in grass or moorland habitats. All three of the transects at Sourhope are in one of these two habitats (Figures 3.15, 3.16, 3.17) whereas at Rothamsted, only one transect in in grassland; the other two transects are in arable and forest habitats respectively (Figures 3.5, 3.6, 3.7). Given the Sourhope transects were in habitats similar to the majority of transects in the study, this could lead to more similar responses in the beetle community than at Rothamsted.

The seasonal trend of the log total response correlates strongly with Temperature (Table 3.21), but much of this relationship is explained by the Month coefficients. Without the inclusion of Month in the model, the relationship with Temperature would be estimated to be greater. As such, the model estimates the effect of Temperature (and other covariates) in addition to the seasonal trend estimated by Month.

As observed in the Rothamsted, Sourhope and multi-site model results, the percentage of residual variance in the null models which was explained by the respective final model was less than 30% for all of the final models fitted. In some cases, the percentage explained was around 16.0%. Therefore there is still a considerable amount of variability left unexplained by the model covariates. If the categorical covariate of Month had been considered to be included in the null model, the deviance explained of the models which included environmental covariates would be lower still. Month was included in all final models in order to capture the seasonal trend. If an environmental covariate were more parsimonious than month in explaining the patterns according to the AICc value, the month variable would have been removed.

Previous studies which were cited where the log total of beetles caught was positively correlated with nitrogen deposition focussed on cases of fertilizer application (Raworth et al., 2004; Batáry et al., 2008). The cited studies looked at the effect over a period of months of applications of up to 100 and 250kg ha^{-1} respectively, which are much larger than the ECN transects, which are typically not affected by such high levels of nitrogen deposition. Thus, the results observed in these models may differ since the observed result is a response to a different range on the nitrogen gradient. The perceived effect of such smallThe perception of such small effects may not accurately portray the true relationship between nitrogen deposition levels and the activity density of the beetles.

If one were not to include Month as a fixed effect in this manner, other covariates, such as temperature, which have a large seasonal trend, would have been fitted as having a much stronger correlation with the beetle response than otherwise. Given that the beetle trend over the year is not primarily a result of temperature, but of the breeding seasons of the carabid species, this could have led to the inference that temperature is solely driving beetle activity density. The primary factor driving seasonal beetle community patterns within a year is the breeding cycle of the beetles themselves. Thus the Month covariate allowed this trend to

be captured while also allowing for variation between years and sites to be explained by the remaining covariates.

Environmental covariates in the final models had weak relationships with the response. Other covariates may have been removed in the model selection process due to outliers conceealing long-standing trends. In order to create a model with higher explanatory performance, the use of finer temporal covariate measurements than monthly estimates may aid the model fit.

Wind is included in the multi-site Shannon index model with a negative coefficient estimated. Some studies have assessed the effect of the preservative (ethylene glycol) in pitfall traps on carabid beetles, with suggestions that the smell could be an attractant for some species (Holopainen, 1992; Woodcock, 2005). Higher wind speeds could spread the odour over a wider area, which may be unattractive for rarer species and increase their catch. Given that the Shannon index response has a negative relationship with wind speed, rarer species could be deterred by the odour, which would reduce the Shannon index value and the effect would be minimal in the log total response. Given that the effect of wind and preservative odour on individual species is not completely understood, it is difficult to infer that that ethylene glycol can effect a change in the beetle community activity.

Information on biotic pressures such as carabid prey or predators has not been included and this may be correlated with carabid population changes. Decreases in prey availability or increases in the numbers of predators may help explain the variation between sites. If predators prefers the most common species, the log total response would be seen to decrease over time, whereas the Shannon index would increase due to the dominant species being reduced at a greater rate than the rarer species. Conversely, if certain dominant species were able to avoid predation, the Shannon index would decrease. It is possible that the relationships are not limited to the prey and predators of beetles, but involve other trophic levels and interactions, which would be too complex to include in this analysis.

Other reasons for the change in beetle community response which have not been taken account of include the size of the beetles themselves. The size of the individual species has not been taken into account when assessing the number of beetles caught. This may have an impact upon the likelihood that a beetle would fall into a trap. Some sites may have lower

number of caught individuals due to the species present at that site being larger themselves. However, given that there is a positive correlation between carabid species size and the estimated distance travelled, this effect may be cancelled out by the higher activity level of larger beetles (Brouwers and Newton, 2009).

As discussed earlier, land management can effect beetle communities greatly (van Dijk and den Boer, 1992); data on the management of the ECN sites has not been incorporated here, but could allow for differences in the diversity of the beetle population to be explained more clearly. Habitat was not used as an explanatory covariate in the models, given that Transect was included as a random effect. However, a detailed stratification of the habitat class at each transect might be able to reveal differing trends within sites.

As stated previously, the sampling period of the *Carabidae* is over approximately 26 weeks from April to November. From the data, this covers the period of greatest activity density adequately, thus providing the most informative data. The pitfall traps are sampled every fortnight, but for periods where activity is very high, it is not known whether the beetles are trapped on a single day or uniformly over the course of a month. Sampling of beetles is time-consuming, laborious and requires expert identification of the various taxa. The collection of finer-scale information, either spatially or temporally than that obtained by the transects at each site would require a greater amount of support in funding and effort.

The scale of the analysis was chosen to be at the Transect-Month level. This was due to the scale of the environmental covariate data, which were available at the Site and Month level. Also, the transects were considered to be independent samples at each site. The data could have been split at a finer-scale, either temporally or spatially, given that there are ten traps in a transect and each traps is emptied every fortnight. Given the traps are spaced 10m apart and the estimated median distance travelled per day by carabids is approximately 2 metres, the traps within each fortnight are not considered independent of each other. If the fortnight responses were used instead of by month, this would not aid the resultant model as extra variability would be included which cannot be explained by the monthly measures of the environmental covariates.

As shown by Fiener and Auerswald (2009) the spatial distribution of rainfall over a small region can vary dramatically, and with some of the sites being located in upland landscapes,

the influence of high windspeed and changes in ground elevation can also lead to differences in precipitation level over short distances. Since the meteorological covariates are measured at single locations, there may be large differences between the measured environmental covariates and the unknown ground truth values at each transect location.

In this analysis, the abiotic data have been estimated at a single point at each site, and associated with the data from each transect at that location. However, the transects are located hundreds of metres apart, and there is potentially large variability associated with the estimated covariate value, for each transect and month. The assumption is that the biotic measurements are the best estimate available of conditions at each transect and are thus themselves precise measurments. Various factors, such as altitude or surrounding habitats can affect the 'ground truth' for the model covariates at each site, and so there is potential for considerable variability which is not included in the model. The accuracy of the covariates is thus unknown. In order to limit the possibility of covariates showing false effects or missing true effects in the model, the spatial uncertainty associated with these covariates can be estimated and the accuracy of the values improved.

There are a large number of possible model extensions which have been discussed, including predator and prey population, land management and habitat information as well as a change of scale in the response and realignment of environmental covariates. In the next chapter, covariate data are measured at a coarser scale than the response. This prompts the possibility of their realignment to the response scale.

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Chapter 4

Plant biodiversity and environmental pressures

4.1 Aim

Almost all plants need sunlight, water and nutrients to develop and grow. Changing levels of these variables can affect plant communities as different species have preferred conditions and can exist best under different combinations of these variables.

The aim of the analysis in this chapter is to create a framework to describe how plant species communities are altered in response to environmental pressures, with specific regard to rainfall and nitrogen deposition. The relationship between the communities and the pressures will then be used to infer the magnitude of the impact of these environmental variables upon the biodiversity response in different habitats.

The plant data used were from the Countryside Survey, using seven of the eight most common Broad Habitats in the survey. Using a range of habitats the overarching effects of environmental variables were fitted, as well as interaction effects with the individual habitats. A statistical model will be developed, which will allow for the flexible fitting of smooth relationships between the these explanatory variables and the model response. The covariates used in these analyses are described in table 4.1 alongside information as to their spatio-temporal scale.

Covariate	Spatial scale	Temporal scale
Easting	100 m accuracy	Stationary
Northing	100 m accuracy	Stationary
Altitude	5 km grid	Stationary
Broad Habitat	CS plot level	CS Survey year
Rainfall	5 km grid	Annual
Nitrogen deposition	1 km grid	30 year average

Table 4.1: Table of covariate data to be used in the modelling of biodiversity measures in this chapter.

In identifying the impact of environmental pressures, the DPSIR framework discussed in chapter 1 is recalled. An impact upon an environmental region is taken to be a response to a number of potential pressures which lead to a specific ecological state. As our response in this case, a biodiversity measure of flora is taken from across the United Kingdom, using data from the surveyed plots within each $1km^2$ CS site.

4.2 Introduction

The Convention on Biological Diversity (CBD) (as referred to in chapter 1) entered into force on 29th December 1993. This was the impetus for the creation in 1994 of the United Kingdom Biodiversity Action Plan (UK BAP). As part of the CBD agreement, all participating countries were mandated to construct a plan for the preservation of biodiversity within their borders. The task of the UK BAP (1994) and the now devolved biodiversity plans is to, "identify, conserve and protect biological diversity".

The Countryside Survey (CS), although initiated in 1978, forms part of the UK BAP and its findings are used in the monitoring of the state of rural habitats across the UK. The CS was set up with the intention to create an 'ecological snapshot' of the state of these habitats at a point in time. It is designed to measure the health or state of the countryside. As part of achieving this end, a wide-scale field survey is conducted; it comprises nearly 600 $1km^2$ sites. The CS, as described by Bunce et al. (1999b), used a stratified random sampling technique to ensure a range of different habitats are surveyed across England, Scotland and Wales. There have been 4 more surveys since the initial study in 1978, in: 1984, 1990, 1998 and most recently in 2007. The data in the field survey were collected from May to November.

In 1978 it was desired to sample from across the range of habitats that exist in Great Britain. However, in order to sample from this range, a large number of 1km^2 sites would need to be assessed, in order to ascertain the type of habitats that existed (Bunce et al., 1975). A preliminary study had been conducted in the Lake District, which involved using map data to ascribe each kilometre square to a land class. This technique was adopted in assessing habitats across GB. However, Britain has an area of approximately $250,000$km^2, so to analyse this amount of data would have been too time-consuming. In order to curtail the number of sites to be assessed and thus those that were available for selection to be sampled, the country was divided into over 1200 225km^2 squares. The central 1km^2 region of these larger squares was analysed, and the land class predicted. From these sites, 32 land classes were created. Eight sites from each land class were then chosen from the analysed 1km^2 squares for the survey.

4.2.1 Previous analyses

There has been extensive literature published on the Countryside Survey; reports published after each survey summarise the main findings in relation to the previous surveys. Results of these studies can be summarised by analysis concerning the area and condition of certain broad habitat types as well as areas of freshwater across Great Britain. In inferring the condition of those areas, reference is made to specific species' abundances, species richness, the change in broad habitat type, and assessment of the realised niche of individual species. For the most recent surveys, the pertinent issues raised are summarised here.

The main objective of the 1990 survey was to record the stock of countryside features in 1990 (Barr et al., 1993), including information on assigned land class, landscape features, habitats and species, in order to:

- Determine change by reference to earlier surveys in 1978 and 1984.
- Provide a firm baseline, in the form of a database of countryside information, against which future changes could be assessed.

The main changes recorded were as follows:

- The proportion of the main semi-natural vegetation types in the British countryside remained constant throughout the late 1980s, but the quality of the vegetation in areas of semi-natural and agricultural land cover declined.

- Loss of habitats and species richness has also occurred in hedges, verges and waterSides but these features were still important reservoirs of plant species, particularly in the lowlands.

- Loss of species and decreases in the quality of vegetation were greater in the lowlands than the uplands.

- The quality of freshwater habitats, as reflected by the invertebrate species they contained in 1990, was also lower in the lowlands.

The 1998 survey noted the following changes in habitat surveyed, as laid out in table 4.2. Haines-Young et al. (2003) also identify the change in identified habitat type of the Countryside Survey plots between the 1984 and 1990 surveys, as identified by the change in plant assemblage that is found there. Thus citing change in habitat area is a summary of the change in species present in the plots assessed in both surveys, given the species present define the broad habitat type assigned to the plot. Between the 1990 and 1998 survey losses in species diversity in Arable and Improved Grassland habitats and respective gains in Acid Grassland regions are noted. These changes in habitat type in the 1980s and species richness in the 1990s are inferred to be possible responses to an increase in nitrogen deposition over the period in question.

In analysis of changes at Countryside Survey sites between 1990 and 1998, Smart et al. (2003a) looked at differences within the aggregate classes to which plants belonged, which were found in the plots in the two aforementioned years of survey. Changes are seen, for instance in the Dwarf Shrub Heath and Bog habitats, which indicate higher nutrient availability and greater disturbance. Possible drivers cited as having caused these changes are increases in grazing pressure and nitrogen deposition. However, it is conceded that further work is needed to explore these relationships. The initial results from the 2007 survey returned information regarding the following questions, detailed in tables 4.3 and 4.4. The issues of interest concern biodiversity, as indicated by species richness and the change in the species present in certain habitats as an indicator of changes in nutrient levels. Changes in grasslands are also mentioned in 1998 as including losses of species important to butterflies. Also listed

in 2007 are the areas covered by broad habitats, and the length and structural condition of hedgerows.

Habitat	Condition
Arable and Horticulture	Species richness increased in arable fields, especially in the boundaries of the fields. Species richness in some arable field boundaries in England and Wales increased by 38%.
Improved and Neutral Grasslands	Species richness continued to decline in the least agriculturally improved grasslands in Great Britain, in some meadows by 8%, including losses of meadow species important for butterflies.
Hedgerows	Following marked losses in the 1980s, there was no significant difference in the 1990 and 1998 estimates of hedgerow length in England and Wales. There is some evidence that losses in the early 1990s have been reversed.
Road verges	Road verges showed evidence of increasing nutrient levels and losses in species richness. Species richness fell by 9% in some road verges in England and Wales.
Woodlands	Broadleaved woodland expanded by 4% in England and Wales and 9% in Scotland between 1990 and 1998. The total area of coniferous woodland in the UK was unchanged.
Acid and Calcareous Grasslands	The area of semi-natural 'acid' and 'calcareous' grasslands fell by 10% and 18% in the UK. There was evidence of increasing nutrient levels or eutrophication in Dwarf Shrub Heath and Bog, suggested by an increase of plant species more typical of lowland grasslands.
Ponds	The number of lowland ponds increased by about 6% between 1990 and 1998 in Great Britain.
Streams	The biological condition of streams and small rivers improved in Great Britain. Over 25% of sites improved in condition and only 2% were downgraded.
Streamside; Fen, Marsh and Swamp	Streamside vegetation became more overgrown, and species richness decreased by 11% in England and Wales. Fen, Marsh and Swamp expanded by 27% in England and Wales and 19% in Scotland.

Table 4.2: Headline messages from the CS 1998 survey (Haines-Young et al., 2000).

Habitat(s)	Recorded effects	
Broad Habitat	Area/Length	Condition
Arable and Horticulture	Decrease in area of 9.1%.	30% species richness increase.
Improved Grassland	Increase in area of 5.4%.	No change witnessed.
Neutral Grassland	Increase in area of 6.0%.	No change witnessed.
Hedgerows	Decrease in length of 6.0%.	48% are in good structural condition.
Broadleaved Woodland	Increase in area of 6.9%.	7.0% species richness decrease.
Coniferous Woodland	No change witnessed.	No change witnessed.
Moorland, Heathland and Bog	Bracken decreased; acid grassland increased; heathland increased by 15%	Increase in competitive species in heathland and bog.
Freshwater habitats	Ponds have increased in number by 11%	Deterioration in condition of ponds since a 1996 survey; improvement in headwater streams.

Table 4.3: Headline messages from the CS 2007 survey (Carey et al., 2008). Periods of change, where not stated, are from 1998 to 2007.

Question of interest	Answer
Which species are increasing or decreasing the most?	Stinging Nettle, Hawthorn and Bramble.
Has botanical diversity in the countryside changed?	Species richness has decreased by 8% between 1978 and 2007.
Have there been detectable effects of air pollution and nutrient inputs on vegetation and soils?	Soil acidity has decreased since 1978, and has decreased also since 1998 for less acidic habitats, broadleaved woodland and neutral grassland. Higher nutrient level-preferring species increased from 1978 to 1998, then decreased to 2007.
Has average Carbon concentration in soils (0-15cm) changed?	No overall change in Carbon concentration has been detected.
Have climate change impacts been detected in the UK countryside?	No plant abundance changes consistent with climate change effects detected.

Table 4.4: Specific questions of interest from the CS 2007 survey (Carey et al., 2008).

In the results of the 2007 survey, plots were assessed with regard to possible changes in plant abundance. If the presence or abundance of certain species are recorded as increasing or decreasing in certain habitats, it can be inferred that conditions have changed, either as a result of environmental pressures, such as deposition, or land use effects. It can be as a result of the same change in an environmental pressure that species with similar traits have positively correlating observed increases or decreases in their presence or abundance. That enviromental pressure which creates preferred conditions for those species is then cited as being potentially responsible for the change in abundance. In analysis of the 1998 CS plots, Smart et al. (2003b) identified an increase in the species coverage of those species with relatively high Ellenberg fertility values. Given that increases are witnessed in the coverage of species with high fertility values, it is inferred that there has been an increase in fertile conditions, and that elevated levels of nitrogen deposition are responsible for this effect. The most probable causes of this deposition increase are cited as being fertilizer application on crops, upland sheep grazing, and atmospheric nitrogen deposits. A direct link between these pressures and the change in species composition is not confirmed.

A similar method of assessing the reason for a change in plant communities can be conducted by taking account of the traits of species which have a significant difference in abundance between two surveys. Smart et al. (2005) assess the extent to which abundances of plants with certain traits have increased or decreased, and ascribes this to the potential environmental impact which could have caused the gradient shift. They conclude that low-fertility habitats show trait changes consistent with increased nutrient availability.

The individual response of plant species to environmental pressures has been analysed, using CS data from the most recent surveys. Smart et al. (2010) used mean Ellenberg scores from species occurrence data to obtain realised niches for over 1000 individual species, in order to provide estimates of habitat suitability, based on the preferred conditions of the community as a whole. Generalised linear models were used to analyse the data. CS data from $4m^2$ plots are used to fit Generalised Linear Models for individual plant species, to determine their realised niche in terms of mean Ellenberg N and F values of all species found in the same locations. Rowe et al. (2011) conducted multiple analyses of CS data from 2007 to test the benefits of using mineralisable nitrogen values as a predictor for the mean Ellenberg N score of a habitat, using a series of differing modelling techniques. GLMs, GAMs and Multiple Adaptive Regression Splines (MARS) were fitted to each species in order to predict habitat suitability based on the mean Ellenberg N score of the species community present at that site.

Maskell et al. (2010) use $4m^2$ CS plot data to link greater nitrogen deposition with a decrease in species richness, with a focus on heathland and grassland habitats. Using a mixed model framework, nitrogen deposition model estimates at the 5km grid square level fitted as an explanatory covariate are found to have a significant relationship with species richness at the plot level. This relationship is negatively correlated in the three Broad Habitats analysed: Acid Grassland, Calcareous Grassland and Heathland. Grazing pressure is also fitted as a model covariate and found to explain significant variation for acid grassland.

These findings of Maskell et al. (2010) concur with a study by Stevens et al. (2010) on Acid Grassland habitats across 153 sites across Western Europe. Data from the Countryside Survey as well as from an independent survey (Stevens et al., 2004) are used together in this analysis using a linear model structure. Species richness in this larger region is also negatively correlated with annual nitrogen deposition values from a 5km grid map. Nitrogen deposition values estimated for specific years were used in this study, but it is conceded that the effects of nitrogen input to a system have a lag attached to them. Given that annual values

and long-term trends in nitrogen deposition are correlated, the annual values are considered a good surrogate for the deposition of nitrogen over the preceding period. This study also assessed the usefulness of the records of certain species as indicators of nitrogen input impacts. Percentage cover of selected species is deemed a more appropriate measure than merely the binary record of presence-absence for inferring change in nitrogen impacts. It is noted that attributing the effects of nitrogen enrichment is difficult, given the data are available at such differing scales.

Stevens et al. (2004) report that Mean annual precipitation and altitude as well as nitrogen deposition are negatively correlated with species richness in a specific calcifugous grassland habitat, using data from sixty-eight sample sites across Great Britain in 2002 and 2003. The significant trends of precipitation and altitude, are due to seven sites in Scotland with increased rainfall levels. Removal of these sites leads to lack of significance for these two covariates.

4.2.2 Critique of literature

In assessing changes to habitat in Great Britain as a response to stated environmental pressures, several studies have already analysed subsets of CS data or plant species data from similar survey. Models of changes in habitats as opposed to individual species models have looked often at changes in species presence or abundance and inferred the presence of the environmental pressure impacting upon the habitat (Smart et al., 2003b). In Rowe et al. (2011), the individual species response is fitted against the mean preferred habitat of the other species present at that site. Most studies use only a limited selection of habitats in the analysis, or do not fit a explicit statistical model to the data; instead the effect of nutrient input is inferred. An example highlighted here cites changes in habitat type at the plot level as the effect of increased nutrient levels (Haines-Young et al., 2003). Initial analysis from the Countryside Survey reports has linked the increase in species indicative of higher nutrient levels and increases in the presence of competitive species as evidence of increase in nutrient input in grasslands, road verges, Dwarf Shrub Heath and Bog (Haines-Young et al., 2000; Carey et al., 2008; Smart et al., 2005, 2003b).

Decreases in species richness have also been negatively correlated with nitrogen deposition and precipitation in grassland habitats, but not in all habitats (Tipping et al., 2013; Maskell et al., 2010; Stevens et al., 2009, 2004). The increase in nutrient levels could be the result of three sources, it is suggested: grazing effects, fertiliser application or nitrogen deposition in

the form of air pollution, or some combination of these three sources (Maskell et al., 2010). If the significant relationships between species richness and precipitation and altitude are due to a small number of sites (Stevens et al., 2004), a stratified sampling process may be necessary, where a specific number of sites are chosen in different parts of the country, in order to avoid sampling bias.

As has been mentioned, indicator values and plant strategies have been used in previous studies to try and pinpoint possible drivers of change in the environment. A necessary development is to attempt to link known, quantifiable drivers and pressures with the observed response, in order to identify causes of the perceived change. Premised by the hypothesis that patterns of change in plant communities may act as responses to anthropogenic drivers, it is noted that spatially and temporally co-located drivers and responses are needed in order to develop understanding of the processes further.

In this chapter, data from the most commonly sampled habitats are fitted against estimates of environmental pressures and abiotic covariate data in statistical frameworks. The fitted covariates allow inference to be made as to the impact of the selected pressures in the chosen habitats. Species richness and presence-absence of specific species have been studied in the literature cited. However, there are other aspects of the biodiversity in a plant community which are not covered by these measures. The importance of measuring biodiversity is in taking account, not of the presence of certain priority habitats but the structural integrity of specific regions.

A biodiversity index is a univariate description of the relative abundances between the species present. A sampled plot can be classified as constituting a specific habitat, but only gives a simple indication of how the countryside is changing as a whole. A diversity measure is a less focussed, more generic approach to population dynamics. Thus, a decrease in species diversity may be observed in a community, which in turn, could lead to the degradation of that community, and this effect would not necessarily be noticed by a species list. Thus, the evenness and heterogeneity of plant communities should be taken into consideration when analysing species communities. The consequence of this is that different response indices will need to be included in the analysis in addition to species richness.

The plot size used is the majority of the literature is the $4m^2$ plot, although the five randomly positioned plots at each CS site contain information on five concentric squares, the largest of which is approximately $14m \times 14m$ in size. The information available at this scale will also be studied in this chapter.

Only the stratified random sample plots, in the CS surveys will be used in this chapter, in order that the plot data is not biased by those plots which appeared of scientific interest and were therefore positioned because of the particular biodiversity to be found there. Thus only the plots whose positions in the CS site were selected randomly, five at each CS site, are analysed.

4.3 Data

In the description of the data to be used, the different variables are described initially, before the explanatory covariates which will be fitted and their spatial resolution. Issues with the data and the challenges they present are discussed also.

4.3.1 Sampling

There are nearly 600 $1km^2$ sites in the CS for each survey year of interest, with up to 5 randomly located square plots at each site. Each of these plots are $200m^2$ in area. Plant species data within the plots are collected as follows. If a specific species is present within a plot, it is recorded and assigned a value of 1. If the area of the plot which that species covers is greater than 5%, then the percentage coverage is estimated, and the species is assigned that value. It is possible that the sum of all species values will be greater than 100, since the coverage regions of two or more species could overlap.

A univariate response for each plot is used here in order to summarise the plant community into a single figure for each plot. Several indices, which are described in chapter 1 will be tested as the response, in order to ascertain how each index is affected by the pressures. The indices to be tested are the Shannon-Wiener index, Simpson's Index of Diversity, Smith

and Wilson's E_{var} index and total species richness. The Shannon and Simpson indices take account of both the heterogeneity and evenness in the species community, the E_{var} index is an evenness index. By recording the number of species in a plot the total species richness response measures only the heterogeneity of a community.

4.3.2 Biodiversity responses

As discussed in chapter 1, there are various possible responses which can be calculated as representative measures of biodiversity. Several of these measures have been used so far, as species richness in chapter 2, log total of individuals and the Shannon index in chapter 3. Four indices will be used initially as the response variable in this analysis, in order to assess their suitability for later models. The responses will be: species richness, the Shannon index, Simpson's Index of Biodiversity and the Evar index. The calculation of these variables is outlined in chapter 1.

4.3.3 Explanatory covariates

The covariates outlined in this section are listed in, and their use in the model can be understood with reference to, table 4.1.

Rainfall

Estimated annual rainfall values are taken from a 5km grid across the country, from Met Office model output. The rainfall estimated at a CS site is a surrogate measure of the water available to the plants present, through both the air and soil. The relationship of a biodiversity index with rainfall helps to explain how spatial differences in biodiversity are the result of variation in rainfall. There is a general gradient of increasing annual estimates from the South-East to the North-West of the country (Figure 4.1). This trend exhibits an interaction with altitude, as areas with higher mean elevation have a greater estimated annual rainfall level. The boxplots show the rainfall for the sampling locations only (Figure 4.2). For each survey, these estimates have a range from around 400 mm to over 3500 mm, with a mean of approximately 1200 mm. The data estimates for 1990 have a smaller median than the other two years and a wider range, exhibited by more extreme values. The 1998 and 2007 data ranges are very similar, with 2007 estimated to have a slightly smaller median.

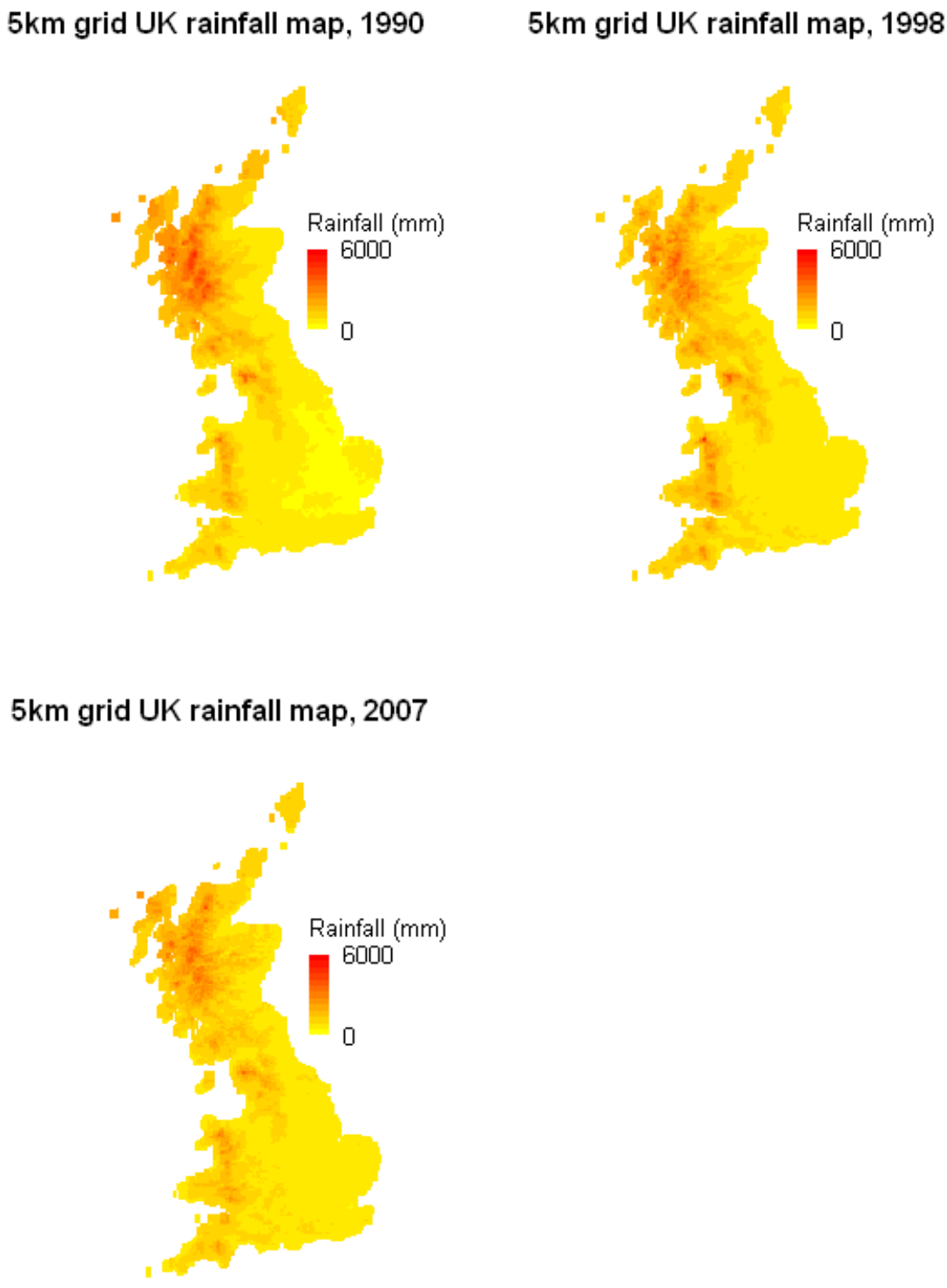

Figure 4.1: Maps of 5km grid Great Britain annual rainfall estimates. A similar spatial pattern is present in all years, where the highest rainfall values are in the most mountainous regions of the north and west of Britain, whereas the lowest values are in the south and east of the country.

Of primary concern is the interpretation of the spatial variability in rainfall and the impact this has on the relationship between the rainfall covariate and the biodiversity response. Inter-survey rainfall trends have not been included; the potential lag effect of rainfall is thus not taken into account. Thus, only one rainfall covariate per survey year is used for every biodiversity response value in the models.

These annual rainfall estimates are not split into monthly estimates, so it is not known what proportion of the rainfall may have occurred before or after the site was surveyed. Rainfall after the survey date would not influence the observed biodiversity response. However, the annual rainfall is an indication of the rainfall in the preceding years at each site, which could have influenced the plant community. Moreover, annual rainfall does vary spatially, and could be effect spatial variability in the plant community response. Thus, the modelled rainfall for the year of survey is used as the covariate for all responses.

As previously noted, previous studies have analysed species richness often, rather than other biodiversity indices such as the Shannon index. Given that the species richness is found to be negatively correlated with rainfall in previous studies (Stevens et al., 2004), the response of other biodiversity indices is to be investigated in this analysis. For instance, if rarer species disappear from a habitat and all other species have no change in their abundance, the Shannon index would decrease, while the relative evenness of the remaining species and the Evar index would increase.

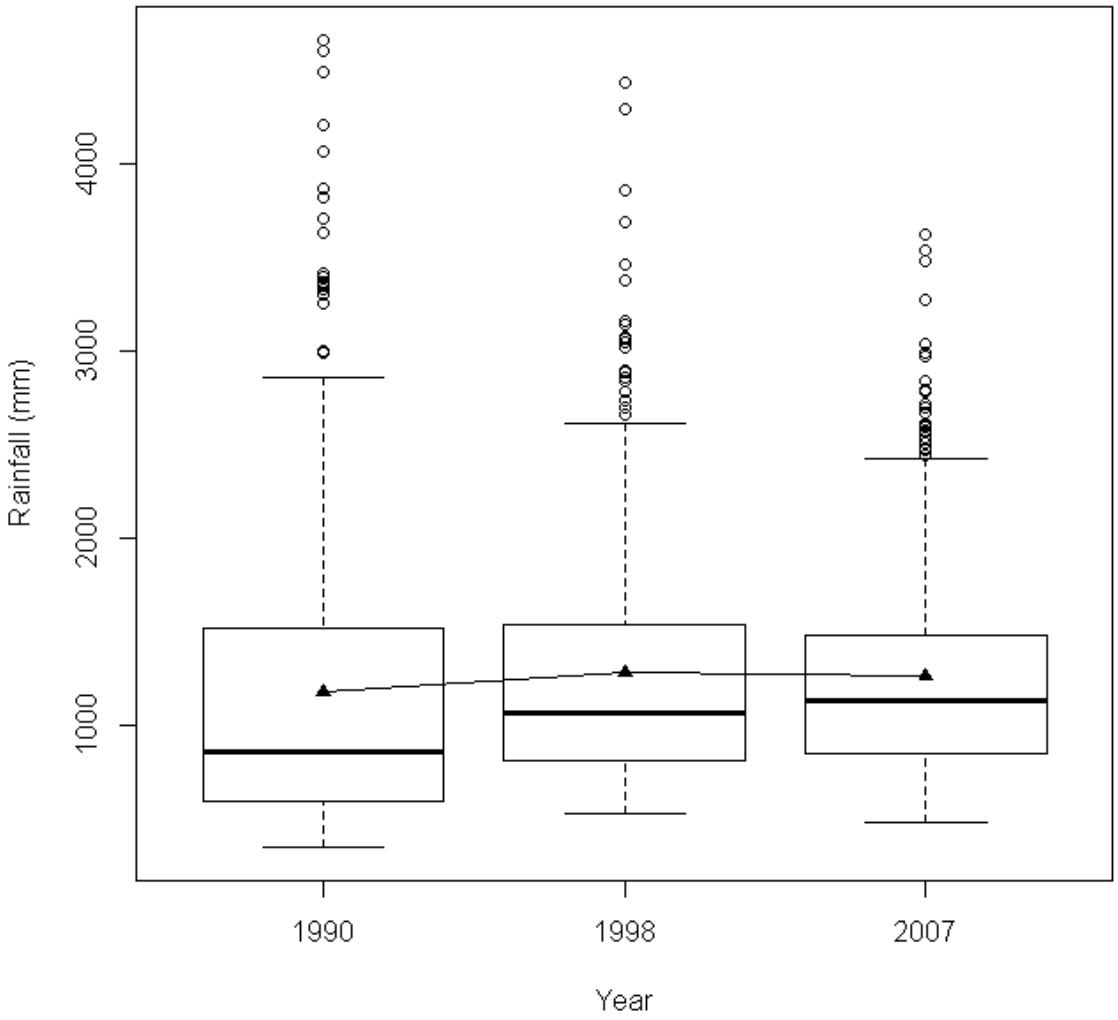

Figure 4.2: UK annual rainfall estimates in figure 4.1 at the location of CS sites. Mean rainfall is indicated by the triangles in each boxplot.

Nitrogen deposition

Total deposition of nitrogen was modelled as an average annual figure at the 1km grid level across the U.K. in the CBED(Concentration Based Estimated Deposition) model (Smith and Fowler, 2001; Smith et al., 2000). Kilograms per hectare per year over the $1km^2$ region are used as units with a range of 0.29 to over 40 kilograms, and a mean of 15 kilograms, shown in the map at figure 4.3. Nitrification of soil can lead to an increase in soil fertility, which benefits species that favour high-nutrient conditions, which in turn could lead to their dominance and a considerable change in community composition. An increase in the coverage of a number of dominant species, relative to the surrounding community will likely be reflected in the biodiversity response as a decrease in the index measure. One reason for the variability in the plant community response may be the difference in soil type. Nitrogen

deposition can also cause soil acidification, when deposited as acid rain, thereby lowering the soil pH and thus changing the conditions for the incumbent plant community. As for the rainfall covariate, relationships fitted in the model between biodiversity and nitrogen deposition will enable the changes in the model index to be understood in light of the changes in the estimated covariate values.

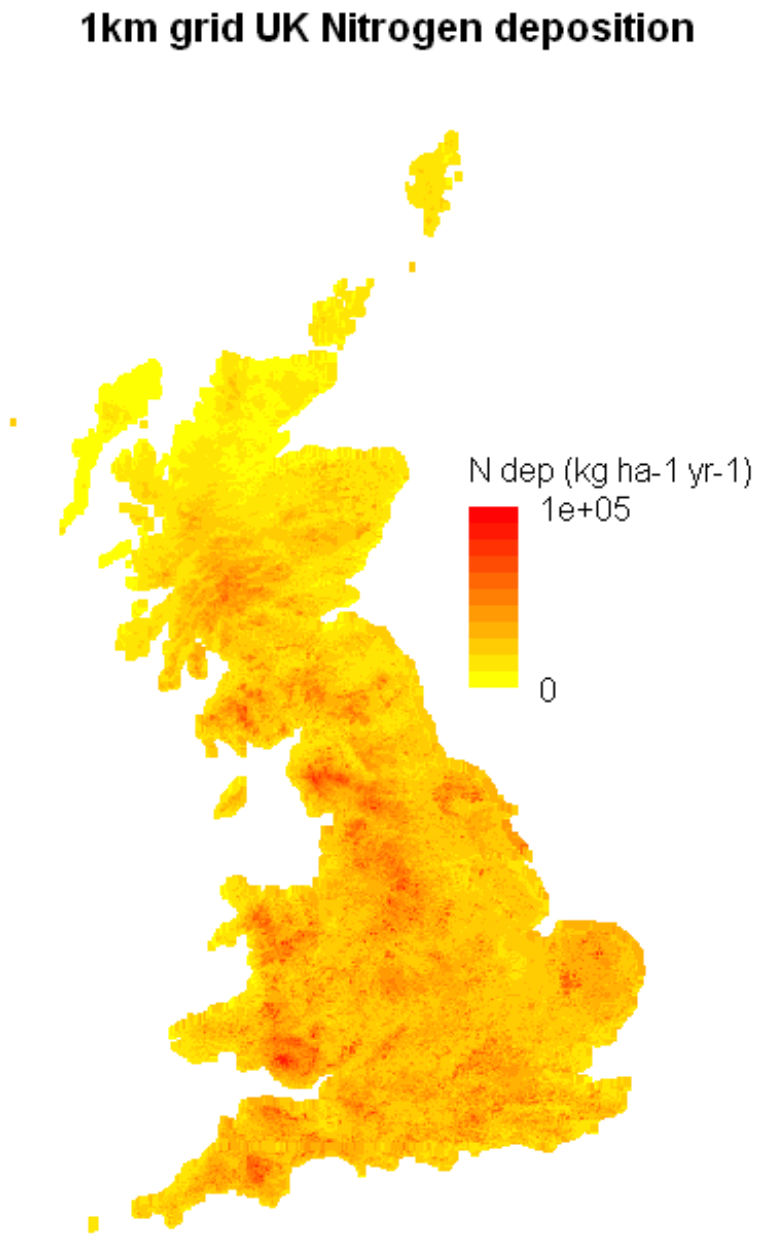

Figure 4.3: Map of the total nitrogen 1km grid square estimates across Great Britain, estimated in kilos per hectare per year.

Spatial locations

Easting and Northing define the positioning of each plot, accurate to 100m. These covariates are used in place of latitude and longitude as the curvature of the earth across the region is not of interest in the analysis and the effect is negligible. Altitude data are recorded as the average of each 25km^2 square (from map data), and have a range from 0 to 1000 metres, with a mean of approximately 175m.

Plot-level data

Plot locations are located using metal plates buried in the ground, so the same area will be surveyed in successive surveys. This allows data from the exact same location to be recorded in each survey, and thus helping to reduce bias in the analysis.

In the Countryside Survey, the broad habitat classes are assessed in land parcels which have a minimum area of 400m^2, as described by Howard et al. (2003) and Firbank et al. (2000). These parcels are defined by reference to several factors: the surrounding physiography, land use methods such as agriculture and forestry, disturbance, soil type and canopy height. As an underlying concept, the Broad Habitat covariate is a surrogate measure of anthropogenic drivers and abiotic pressures. Broad Habitat as a factor is useful in distinguishing the effect of the different habitats on the diversity found within them. There are 23 broad habitats within the CS; the eight most common types are listed in table 4.5. Data from these habitat types will be studied further in the analysis.

Land use can vary within habitats; land management varies within land use. Changes within either land use, land management or both can have effects on the plant community at the sub-habitat level; these effects will not necessarily correlate with habitat and thus any effect may be unexplained by the model covariates or cause a spurious link with one or more covariates.

Management effects in this case denote changes to the environment along one of two gradients: nutrient addition and disturbance. It is along these two scales that plant strategy is defined, as discussed in chapter 1. Change in these factors is what characterises land man-

agement. Within habitats, management of the land can affect the biodiversity of a plot. This is usually an inhibiting factor, as the excessive nutrients used in farming methods, for instance, allow competitive species to dominate; disturbance of land allows ruderal species to take advantage.

Data issues

Initially, the covariates of altitude, total Nitrogen deposition and rainfall are estimated at a coarser spatial scale than the locations of the CS plots. The CS sites then aligned with those $1km^2$ nitrogen and $5km^2$ rainfall squares within which they are positioned. Since the $1km^2$ squares align with the 5km and other 1km grids, then for each sample site and thus each plot, there is only one value of each explanatory variable with which it is associated. Therefore, this simple structure assumes that all sites within the same 5km region are associated with the same value of that respective explanatory variable. The problem of closely-located sites should not occur often, since, as stated previously, the original sites chosen in 1978 were located on a 15km grid. In later years, extra sites have been set up in priority habitats that have been cited as needing a greater intensity of sampling. As a result of this, they are more likely to be situated close to one another. In addition to this uneven distribution of sites, there is not only a greater density of sites towards the north and west of the U.K., but sites located in these rare, marginalised habitats will be more likely to be close together, and thus be influenced by the same explanatory variables which are only available at a relatively coarse grain. The impact of rainfall and nitrogen is likely to vary according to the habitat upon which it falls. Thus, the biodiversity response is likely to differ accordingly. In the model, an interaction term between rainfall and plot habitat as a categorical factor will be included to assess the differences in the relationships.

4.4 Analysis

4.4.1 Exploratory analysis

Figure 4.4 shows the scatterplots of possible biodiversity responses to be used in the model. A larger Shannon index value denotes a more diverse plot; there are a lot of plots with all

species only having an abundance of 1, which return an index value of 0. This is due to the index's lower bound at 0. Some degree of positive correlation is evident between each of the indices; the strongest correlation appears to be between total species richness and the Shannon index.

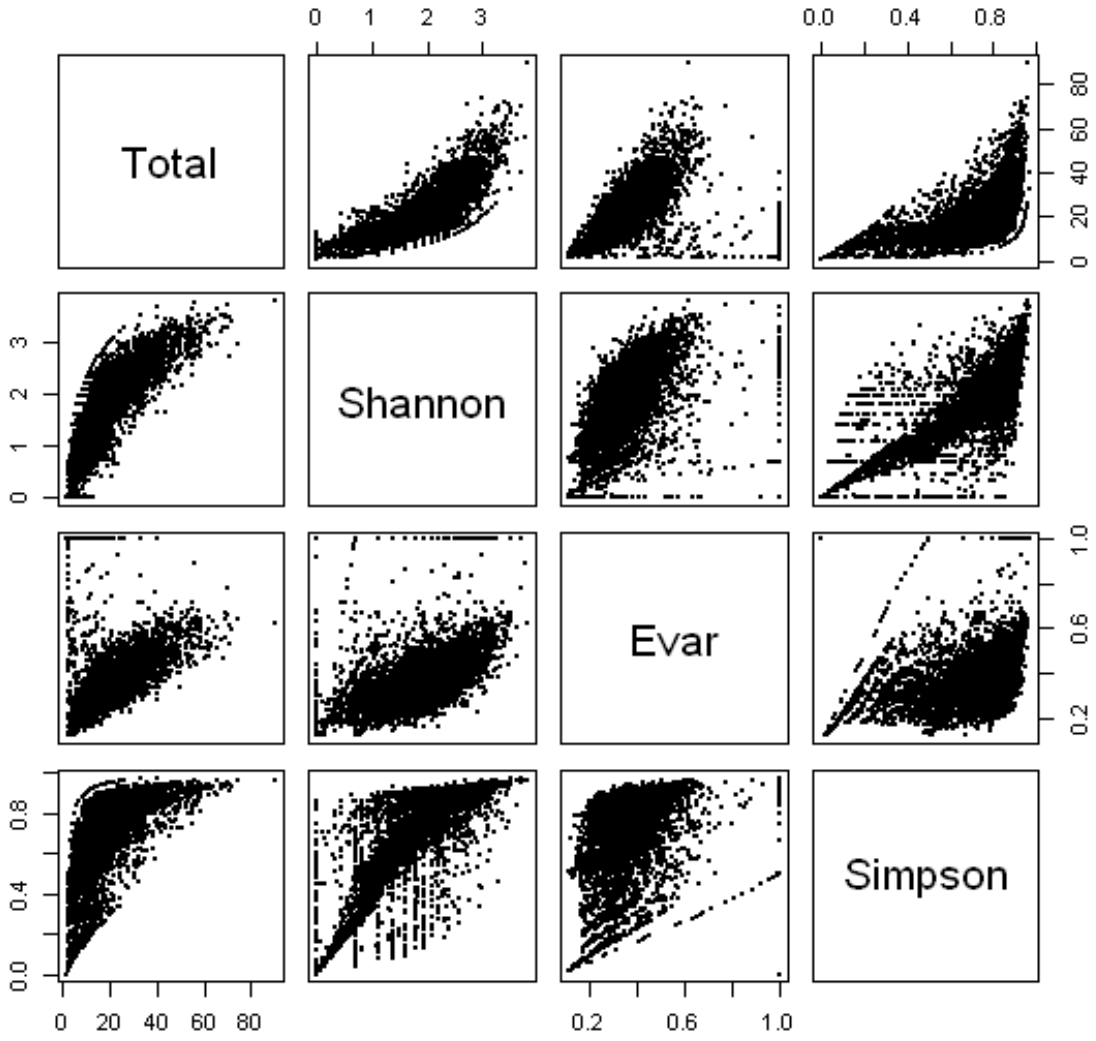

Figure 4.4: Biodiversity responses for CS sampling plots in all years. The indices depicted are: total species richness, the Shannon-Wiener index, Smith and Wilson's E_{var} index and Simpson's Index of Diversity. There is a positive correlation between all pairs of indices, but a large amount of variation also, for example between the Simpson and E_{var} indices.

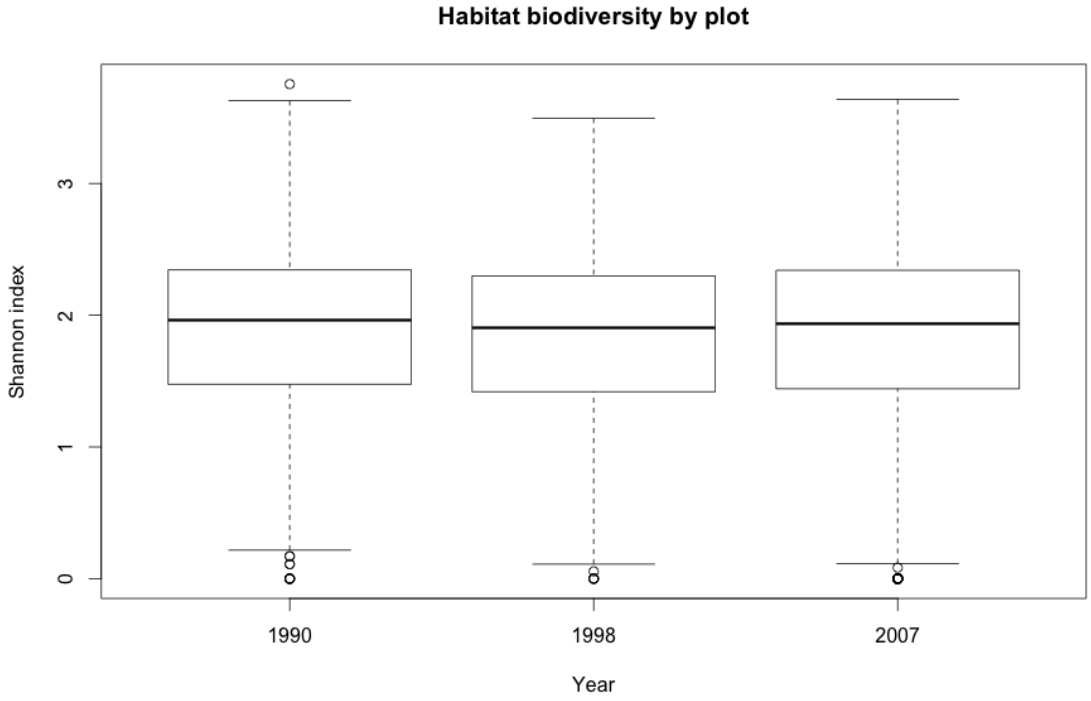

Figure 4.5: Shannon Diversity of CS plots, by year.

The boxplots in figure 4.5 show the trend in Shannon-Wiener plot diversity across the three surveys of interest. There is a slight decrease and subsequent increase over time in the median value. The boxplots in figure 4.6 show the Shannon-Wiener diversity for each distinct habitat.

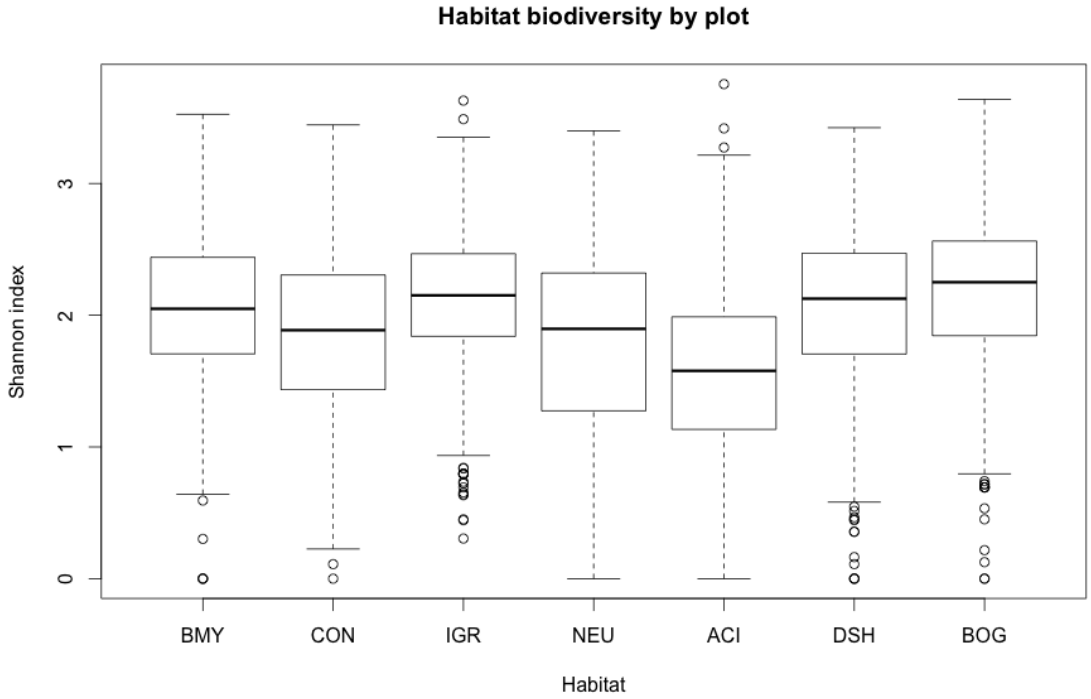

Figure 4.6: Shannon Diversity of CS plots, by habitat. The habitats to be analysed in this case study are BMY: Broadleaved, Mixed and Yew Woodland, CON: Coniferous Woodland, IGR: Improved Grassland, NEU: Neutral Grassland, ACI: Acid Grassland, DSH: Dwarf Shrub Heath and BOG: Bog.

Broad Habitat type	Code	1990	1998	2007
Broadleaved, Mixed and Yew Woodland	BMY	133	136	135
Coniferous Woodland	CON	160	153	143
Improved Grassland	IGR	521	450	398
Neutral Grassland	NEU	164	207	205
Acid Grassland	ACI	191	141	145
Dwarf Shrub Heath	DSH	159	112	115
Bog	BOG	201	200	200

Table 4.5: Table of the number of plots of each of the seven main habitat types used in this analysis.

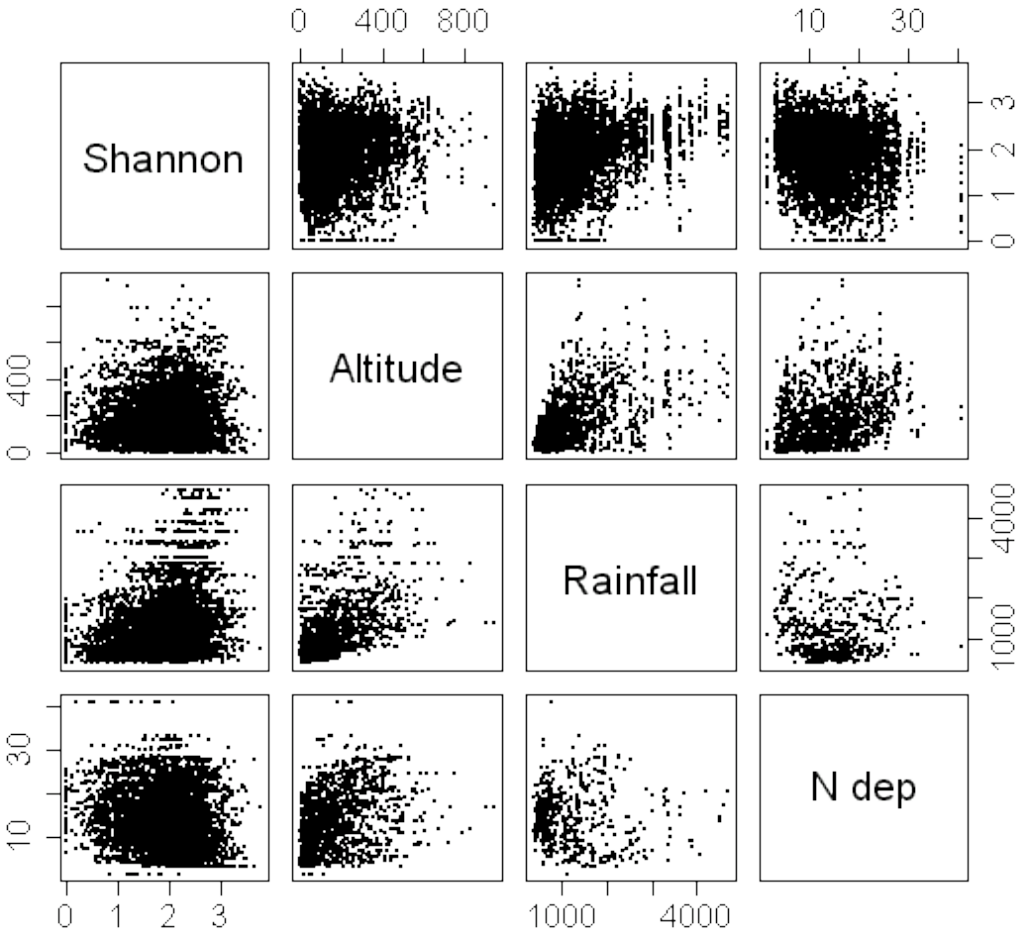

Figure 4.7: Shannon Diversity of CS plots and environmental covariates for biodiversity plots in all years. Altitude is measured in metres above sea level, rainfall is measured in milimetres and nitrogen deposition is measured in kg per hectare per year.

There is no clear trend exhibited for the Shannon index with the explanatory covariates in figure 4.7. From the other scatterplots, rainfall appears to be partially correlated with altitude, and inversely correlated with easting. In figure 4.3 nitrogen deposition shows a slight correlation with both easting and northing, with its highest values in the south and more upland areas in the west of the country. Up to this point, most of the models fitted have been linear models. The exploratory analysis shows no distinct linear relationships between the covariates and response. The previously displayed scatterplots show only each covariate individually plotted against the biodiversity indices; the additive effect of these covariates could be non-linear in form but indiscernible from these plots. In order to investigate the

possibility of non-linear trends, an additive model will be utilised in this analysis which allows a more flexible fit of certain covariates to the response.

Subsetting the data by habitat, individual habitat analysis will allow estimation of separate coefficients for various habitats and inference to be made on what is driving change in each respective habitat. In order to allow for coefficient estimates to be calculated as precisely as possible, it is required that there be a large number of responses for each habitat to be used in the proceeding models. The most common habitats and the number of plots of each habitat sampled in each survey year are listed in table 4.5: Broadleaved, Mixed and Yew woodland; Coniferous woodland; Improved grassland; Neutral grassland; Acid grassland; Dwarf Shrub Heath and Bog. Thus, these seven data subsets will be analysed separately. The number of Arable plots was greatest, but these data are omitted from the analysis, since the responses for this habitat were deemed too susceptible to the effects of land use, that their inclusion may hamper or distort the trend in other habitat responses.

4.5 Method

Given the lack of direct linear relationships between the covariates and the response in the exploratory graphs, an additive model structure will be utilised in the analysis to allow for non-linear regression lines to be fitted. This does not exclude the possibility of the covariates which are fitted using splines been fitted as linear terms; this is outlined in section 4.5.1 The next subsection details the fitting of the additive model and the chocie of covariates to in the model selection procedure.

4.5.1 Additive Model

The structure of an Additive Model (AM) is:

$$y_i = \mathbf{X}_i\beta + s_1(x_{1i}) + s_2(x_{2i}, x_{3i}) + \cdots + \varepsilon_i, \tag{4.1}$$

where y_i is the response variable, X_i is the corresponding row of linearly-modelled covariates, the $s_j(\cdot)$ are smoothing spline functions, ε_i is the error term, here distributed as $\varepsilon \sim N(\mu_\varepsilon, \sigma_\varepsilon)$, as outlined by Wood (2006).

Additive models are fit by Penalized-Iteratively Reweighted Least Squares (P-IRLS). Here we seek to maximise a penalised log-likelihood function:

$$l_P(\beta) = l(\beta) - \frac{1}{2}\beta^T \mathbf{S}\beta, \tag{4.2}$$

where $l(\beta) = \log(L(\beta))$ is the log likelihood function with $L(\beta)$ as in 2.4 and β the vector of coefficients. $\mathbf{S} = \sum_j \lambda_j S_j$, where the S_j are known coefficients and the λ_j are unknown penalty terms corresponding to each $s_j(\cdot)$ function. The λ_j are chosen by minimising the Generalised Cross Validation (GCV) score, which can be written:

$$v_g = \frac{n \parallel \mathbf{y} - \hat{\mu} \parallel^2}{[n - tr(\mathbf{A})]^2} \tag{4.3}$$

In the above equation, n is the number of responses, $\mathbf{y}$ is the vector of response data, $\hat{\mu}$ is the vector of fitted values and $\mathbf{A}$ is the influence matrix, calculated as $\mathbf{A} = \mathbf{X}\left(\mathbf{X}^T\mathbf{X} + \mathbf{S}\right)^{-1}\mathbf{X}^T$. The model is fitted by maximising the penalised likelihood in equation 4.2, using the Newton-Raphson method, then calculating the GCV score upon convergence, as described by Wood (2006).

Model selection example

In order to show the workings of the backward selection method, a preliminary analysis of a particular habitat and response are highlighted and the procedure for obtaining the resultant model is shown. Backward selection affords a descriptive model results reflecting the relationships between covariates and response in the dataset. The difference in the additive model framework is that covariates can be fitted as either smoothers or linearly. If the final model contains a smoothed covariate with estimated degrees of freedom associated equal to 1, this is an indication that the fitted relationship is actually linear and the model is refitted with that covariate as linear, in order to obtain the estimated coefficient of the line in the model result. Where a covariate is fitted nonlinearly and its estimated associated degrees of

freedom are not equal to 1, the simplified model is not refitted with that covariate as linear, but tested only with or without the term with regard to the AICc value as outlined in chapter 1.

Here, the Improved Grassland habitat plots are modelled using the Shannon index response. Firstly, variables need to be considered as to their inclusion in the initial model.

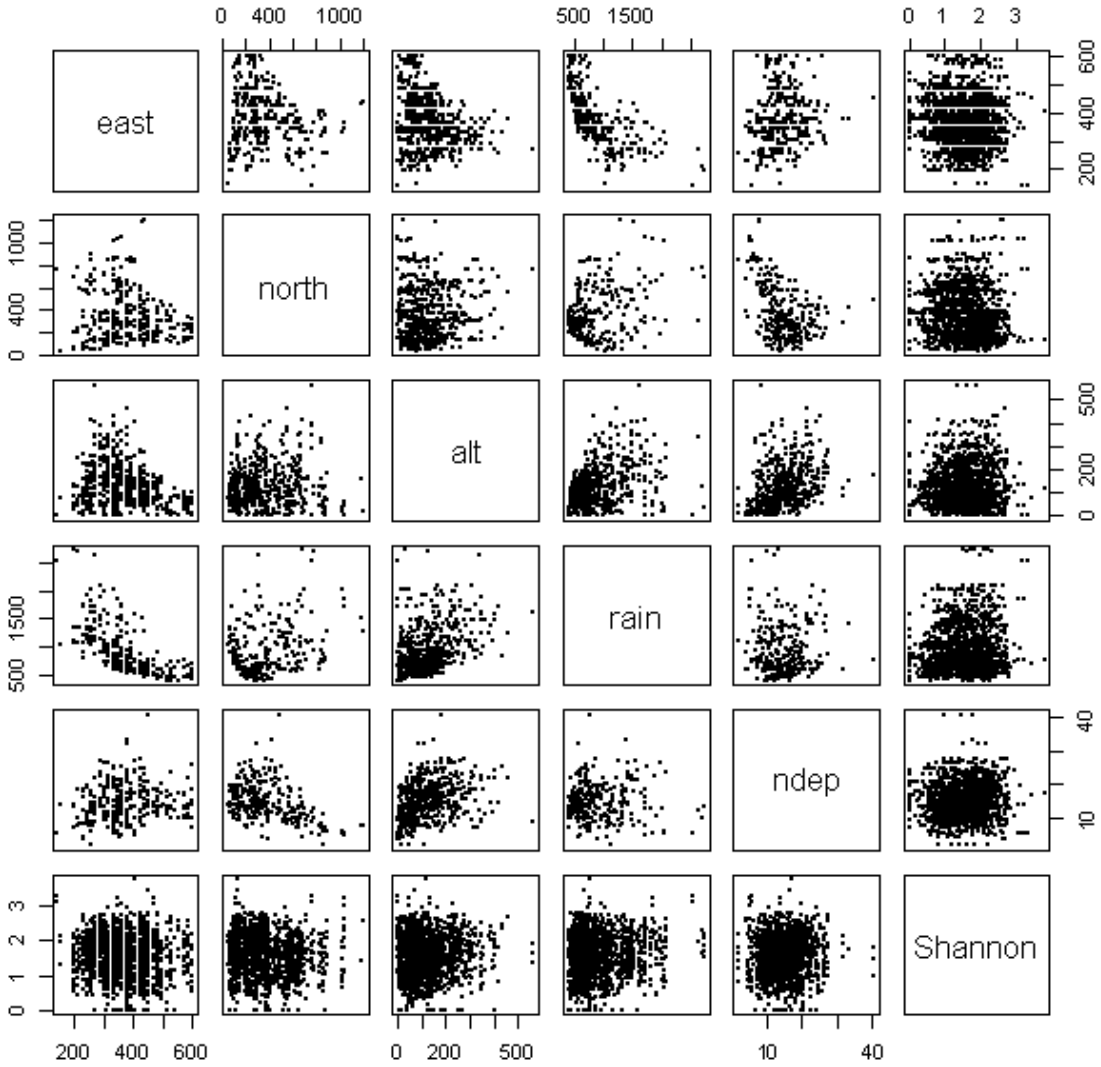

Figure 4.8: Shannon diversity of CS plots and environmental covariates for inclusion in the Improved Grassland model. Easting and Northing are measured in kilometres from the South-West tip of Britain, Altitude is metres above sea level, rain is millimetres of rain per year and nitrogen deposition is kilograms per hectare per year.

Thus, the process is begun by looking at the scatterplots of all data in the model (figure 4.8). From these graphs, there does not appear to be any strong relationship for any of the possible explanatory variables, but given the large number of responses in the model, it is anticipated that significant trends will prove themselves to be present in the eventual model, and hence the analysis has high power. The presence of potential weaker relationships between the covariates and response will be explored. East and North variables are considered as a joint smoother also, in order to allow the trend over the country to be assessed coherently. Rain will be tested as a smoothed covariate in the model. Nitrogen deposition and altitude will also be tested as a univariate smoothing terms. Year will be inserted as a linear term, given the inability of the model to create a smoother over the three distinct data values for this covariate: the three years of survey (1990, 1998 and 2007). The initial model to be tested is as follows:

$$S_{jk} = s_1\left(E_j, N_j\right) + s_2\left(A_j\right) + s_3\left(R_{jk}\right) + s_4\left(D_j\right) + \beta_1 Y_k + \beta_2 + \varepsilon_{jk}, \tag{4.4}$$

where S_jk is the Shannon index of the jth plot in the kth year, Easting and Northing are represented by the E_j and N_j terms, R_{jk} and A_j are rainfall and altitude respectively, D_i denotes nitrogen deposition Y_k is the year, and the spline functions $s_i(\cdot)$ are fitted for each covariate i apart from Year. The β_1 term is the coefficient of Year in order to test for trend across years and β_2 is the intercept. The $\varepsilon_{jk} \sim N\left(0, \sigma_\varepsilon^2\right)$ term represents a normally distributed error term.

Model No.	Model covariates	AICc	Dev. expl.
1	s(E,N) + s(A) + s(R) + s(D) + Y	2383.9	10.2%
2	**s(E,N) + s(A) + s(R) + s(D)**	**2383.6**	**10.0%**
3	s(E,N) + s(A) + s(R) + Y	2384.9	9.3%
4	s(E,N) + s(R) + s(D) + Y	2384.1	9.3%
5	s(A) + s(R) + s(D) + Y	2455.5	2.3%
6	s(E,N) + s(A) + s(R)	2384.6	10.0%
7	s(E,N) + s(R) + s(D)	2383.9	9.1%
8	s(E,N) + s(A) + s(D)	2385.4	9.1%
9	s(A) + s(R) + s(D)	2455.2	1.6%

Table 4.6: Table of the Improved Grassland model fitting process, with the first model being the initial model tested. The $s(\cdot)$ functions indicate where a covariate was fitted to be smooth. Model 2 is the selected model, with all covariates apart from Year remaining in the model. A null model is fitted with a mean component, in order to calculate the deviance explained in the tested models.

Covariate	β_i estimate	Std. Error	P-value
(Intercept)	1.32	0.08	-
Rain (mm)	1.53×10^{-4}	6.6×10^{-5}	0.02
N dep (kg ha^{-1}yr^{-1})	5.14×10^{-3}	4.44×10^{-3}	0.25

Covariate	Est. d.f.	P-value
s(A)	2.50	0.44
s(E, N)	16.01	<0.01

Table 4.7: Chosen model for the Improved Grassland Shannon index response, where $s(\cdot)$ indicates a smoother. The estimates given for the Altitude and East-North smoothers are the respective estimated degrees of freedom, as shown in figure 4.9.

Table 4.7 gives the result of the chosen fitted model for the Improved Grassland with Shannon index response. The trend for Rainfall indicates that for every metre increase in rainfall, the Shannon index increases by approximately 0.15 on the Shannon index scale. Likewise for nitrogen, for every 10 kilogram increase in the estimated nitrogen deposition in the 1km^2 grid square, the estimated Shannon index value increases by just about a twentieth of an Shannon index value. The East-North smoother shows a bivariate trend in the index response of lower values in the South-East and South-West of Great Britain to the North-West. The lowest contour in the East and South-West of the country has a value of -0.2, with a gradient towards the 0.6 contour in the North-West; an estimated gradient of under 1 index value across the region of interest. This effect may be indicative of several possible pressures:

e.g. unincluded meteorological effects such as temperature or biotic pressures such as the invasion of competitive species or intensification of land use.

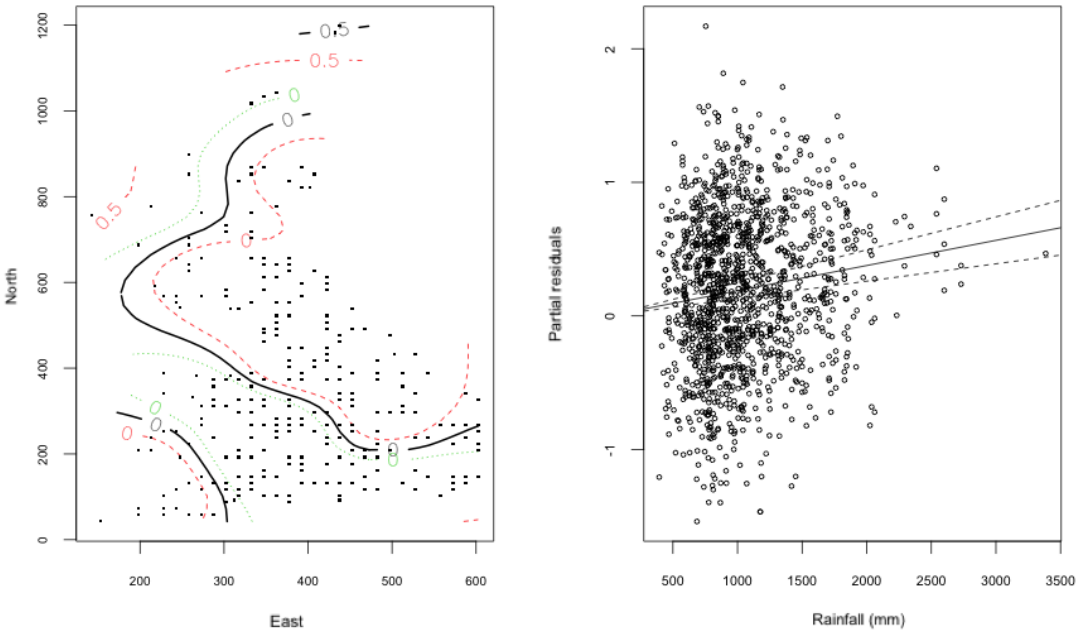

Figure 4.9: Smoothing splines for the chosen Improved Grassland Shannon index model, for Easting and Northing and for Rainfall, with standard error bars shown as dotted lines. Despite the smoothing spline not being restricted by the model structure, the Rainfall smoothing spline was automatically fit to be linear.

The chosen model in figure 4.9 shows the fitted splines obtained for the Improved Grassland habitat sites. The spatial smoother shows the highest diversity to be in the Northwest of Scotland, with the lowest diversity in Northern and Southwestern England. Rainfall shows a positive correlation with the Shannon index response, but there is a large amount of uncertainty surrounding the regression line. There is still a large amount of unexplained variability in the final model, even though four covariates are included (Table 4.6). Diagnostic plots in figure 4.10 show no violation of the model distributional assumptions.

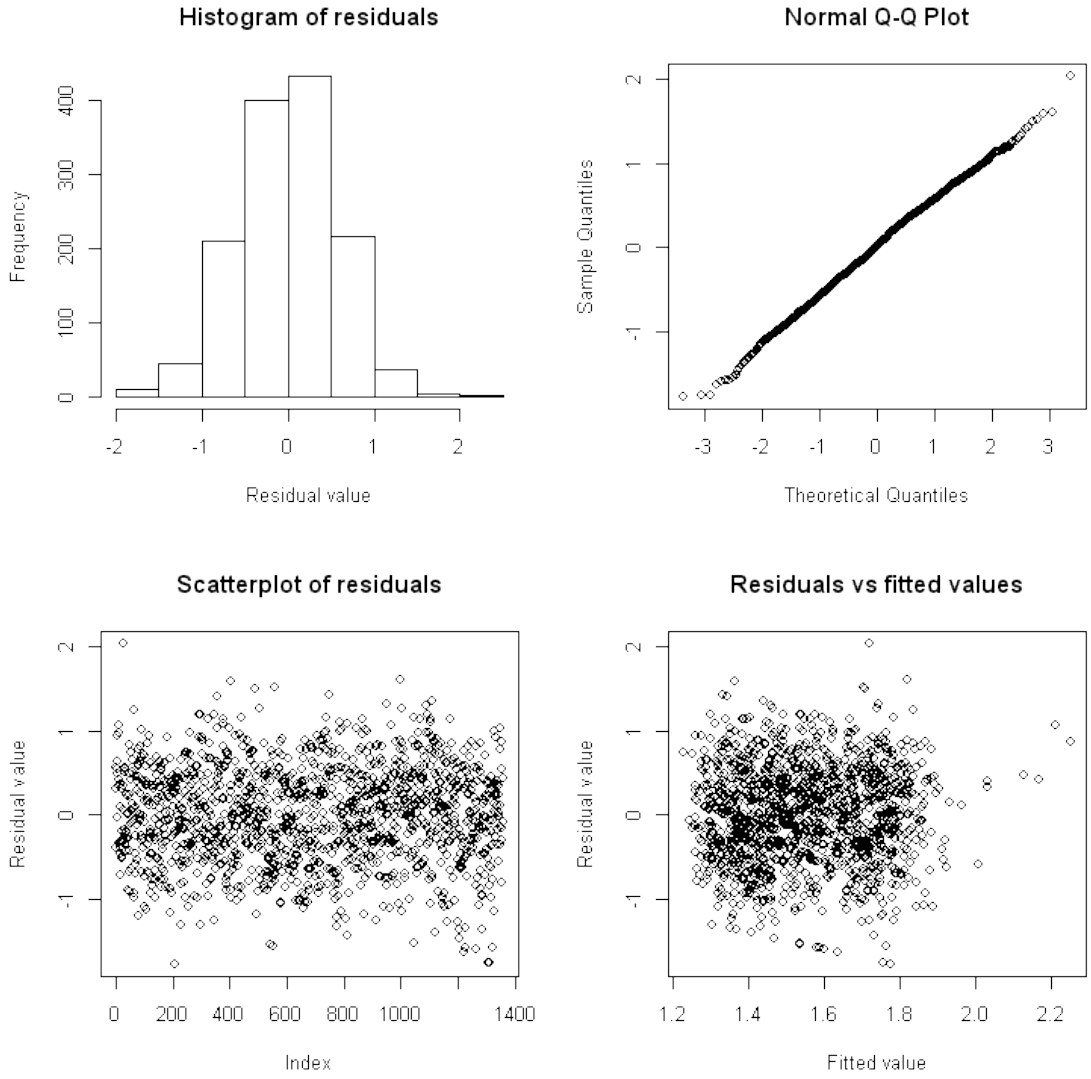

Figure 4.10: Diagnostic plots for Shannon response, Improved Grassland model 2. There does not appear to be any indication of violation of the model assumptions.

Tables 4.8-4.14 give the chosen models for each of the four model responses and 8 most common habitats. A null model for each habitat and biodiversity response is fitted with a mean component as sole fixed effect, in order to calculate the deviance explained by each final model relative to the respective null model. The most commonly appearing trend between the sites is the Easting-Northing smoother, which is present in all but three models. Given the degree of correlation between the indices in figure 4.4, it is not unexpected that where a spatial trend is present in the final model for one possible response index, that there is a strong spatial trend for the other three indices. Given the differing responses between

habitats, an all-site model, allowing for interactions with the factor of Broad Habitat will be fitted, based on data from seven of the eight most common habitats.

Response	Chosen model	Deviance explained
Evar	s(A) + s(E, N) + Y	24.5%
Shannon	s(D) + s(R) + s(E, N)	32.7%
Simpson	s(D) + s(R) + s(E, N) + Y	34.4%
Total	s(D) + s(R) + s(E, N) + Y	46.6%

Table 4.8: Broadleaved, Mixed and Yew Woodland AM final models.

Response	Chosen model	Deviance explained
Evar	s(A) + s(D) + Y	10.1%
Shannon	s(A) + s(D) + s(E, N)	25.2%
Simpson	s(A) + s(D) + s(R) + s(E, N) + Y	26.0%
Total	s(A) + s(D) + s(E, N)	35.2%

Table 4.9: Coniferous Woodland AM final models.

Response	Chosen model	Deviance explained
Evar	Y	2.8%
Shannon	s(A) + s(D) + s(E, N) + Y	10.0%
Simpson	s(A) + s(D) + s(E, N) + Y	10.2%
Total	s(A) + s(D) + s(R) + s(E, N) + Y	19.4%

Table 4.10: Improved Grassland AM final models.

Response	Chosen model	Deviance explained
Evar	s(A) + s(D) + s(R) + Y	11.3%
Shannon	s(D) + s(E, N) + Y	13.0%
Simpson	s(A) + s(D) + s(R)	17.5%
Total	s(D) + s(R) + s(E, N) + Y	18.8%

Table 4.11: Neutral Grassland AM final models.

Response	Chosen model	Deviance explained
Evar	s(D) + s(R) + s(E, N) + Y	32.2%
Shannon	s(D) + s(R) + s(E, N) + Y	33.7%
Simpson	s(D) + s(R) + s(E, N) + Y	36.5%
Total	s(A) + s(D) + s(R) + s(E, N)	46.5%

Table 4.12: Acid Grassland AM final models.

Response	Chosen model	Deviance explained
Evar	s(E, N) + Y	25.0%
Shannon	s(A) + s(R) + s(E, N)	44.0%
Simpson	s(A) + s(D) + s(E, N) + Y	40.6%
Total	s(A) + s(R) + s(E, N)	56.1%

Table 4.13: Dwarf Shrub Heath AM final models.

Response	Chosen model	Deviance explained
Evar	s(A) + s(D) + s(R) + s(E, N) + Y	35.3%
Shannon	s(A) + s(D) + s(R) + s(E, N) + Y	35.4%
Simpson	s(A) + s(D) + s(R) + s(E, N)	21.3%
Total	s(A) + s(D) + s(R) + s(E, N) + Y	38.5%

Table 4.14: Bog AM final models.

The total species richness model has the highest value of deviance explained relative to the null model for each habitat and response respectively; the E_{var} models have the least for most habitats. The Shannon and Simpson models return similar values of explained deviance. The covariates of rainfall, nitrogen deposition, Easting and Northing are most commonly included in the final models. Although the Shannon index response does not return the largest deviance explained in all habitats, the diagnostic plots for this response show the least violation of model assumptions. Therefore, the Shannon index will be used as the sole response in the next modelling stage. The covariates selected in each of the Shannon models are not always identical. In the next stage, all seven habitats will be modelled together, to allow the interaction effect of habitat to be compared more easily.

4.5.2 All-habitat model

In this section, a model for seven of the most common habitats which were sampled will be fitted. In a similar manner to the beetle models in chapter 3, the model process will allow for interactions between meteorological and biogeochemical effects and the habitat in which the sampling plot is positioned. In this framework, the differing relationships between habitats are more easily identified and compared.

The presence of interaction is evident when a change is perceived in the relationship between the explanatory variable and response, with respect to another covariate. There is a need to take account of various interaction effects within the data, in order to understand how different habitats are affected by respective environmental drivers and pressures. The abiotic pressure interaction plots for rainfall and nitrogen are shown in figures 4.11 and 4.12. This allows the comparison to be shown between the Shannon diversity response and rainfall and nitrogen respectively, based on the separation by Broad Habitat and by year.

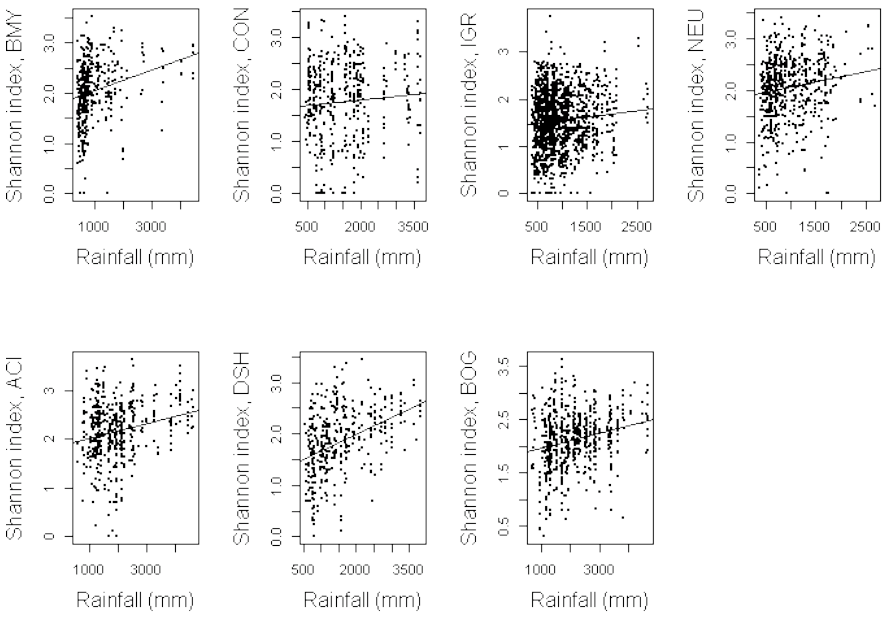

Figure 4.11: Scatterplots of Shannon index versus Rainfall, by Broad Habitat. The line on each graph is the simple linear regression of the shannon index on rainfall, for each individual habitat. BMY: Broadleaved, Mixed and Yew Woodland, CON: Coniferous Woodland, IGR: Improved Grassland, NEU: Neutral Grassland, ACI: Acid Grassland, DSH: Dwarf Shrub Heath and BOG: Bog.

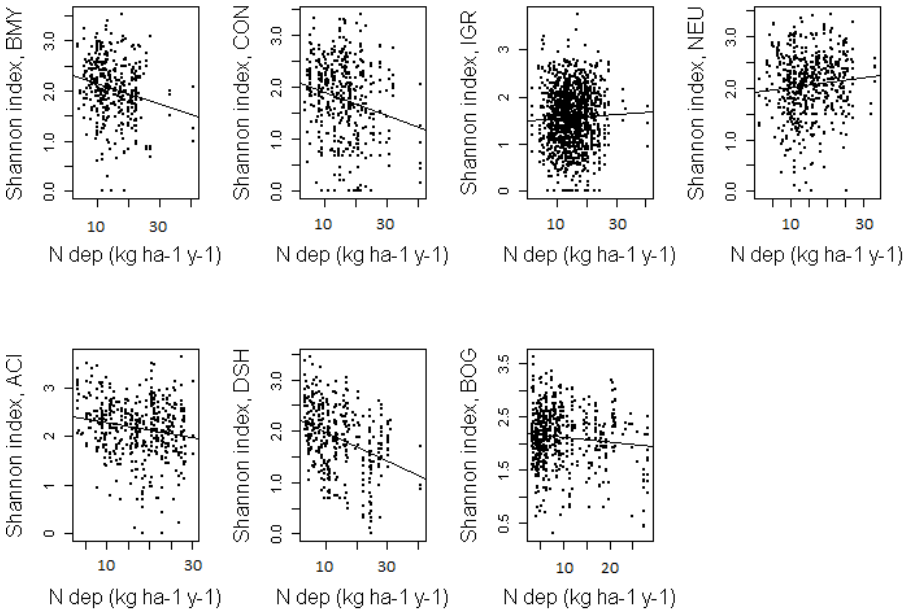

Figure 4.12: Scatterplots of Shannon index versus nitrogen deposition, by Broad Habitat. The line on each graph is the simple linear regression of the shannon index on nitrogen deposition, for each individual habitat. BMY: Broadleaved, Mixed and Yew Woodland, CON: Coniferous Woodland, IGR: Improved Grassland, NEU: Neutral Grassland, ACI: Acid Grassland, DSH: Dwarf Shrub Heath and BOG: Bog.

The choice is taken to add in interaction terms for nitrogen deposition and Rainfall with regard to Broad Habitat, with the view that for a large number of the sites, this is a realistic estimate of what is actually taking place; the effect that nitrogen has is dependent upon the plant structure upon which it is deposited.

Following on from the choices of interaction to be tested in the model, backward selection is again used to find a suitable structure for the AM with Broad Habitat as an fixed effect in order to test for interaction with rainfall and nitrogen deposition. The initial model tested is:

$$S_{ijk} = s_1\left(E_i j, N_i j\right) + s_2\left(A_i\right) + s_3\left(R_{ik} : BH_{ijk}\right) + s_4\left(D_i : BH_{ijk}\right) + \beta_1 BH_{ijk} + \beta_2 Y_k + \beta_3 + \varepsilon_{ijk}, \tag{4.5}$$

where S_{ijk} is the Shannon index response at plot j at site i in year k. The other covariates are defined as in equation 4.4. The spline functions $s_{\cdot}(\cdot)$ are fitted for each covariate or interaction of covariates. The ':' denotes an interaction effect between two variables. The error term ε_{ijk} is normally distributed. The model obtained at the end of this process is shown in table 4.15.

Model	AM with E,N			AM, no E,N		
Covariate	β_{ij} est.	S.E.	P-value	β est.	S.E.	P-value
BMY	2.16	0.04	<0.01	2.18	0.04	<0.01
CON	1.82	0.04	<0.01	1.82	0.04	<0.01
IGR	1.67	0.04	<0.01	1.67	0.04	<0.01
NEU	2.18	0.04	0.79	2.18	0.09	1
ACI	2.16	0.04	0.97	2.20	0.06	0.77
DSH	1.80	0.04	<0.01	1.80	0.04	<0.01
BOG	2.12	0.09	0.66	2.29	0.18	0.54
Y	-2.59×10^{-3}	1.29×10^{-3}	0.08	-0.003	0.001	0.03

Model effect	Est. d.f.	P-value	Est. d.f.	P-value
s(R)	2.92	0.04	1.00	0.83
s(R:BMY)	2.71	0.01	4.41	<0.01
s(R:CON)	6.10	<0.01	6.32	<0.01
s(R:IGR)	2.99	0.22	3.04	0.34
s(R:NEU)	1.00	0.35	3.99	0.18
s(R:ACI)	1.00	0.74	4.53	0.07
s(R:DSH)	2.63	0.15	2.88	0.22
s(R:BOG)	7.21	0.09	1.00	0.81
s(D)	1.00	0.94	1.00	0.98
s(D:BMY)	1.00	0.71	1.00	0.93
s(D:CON)	1.00	0.59	1.83	0.29
s(D:IGR)	1.00	0.92	1.00	0.95
s(D:NEU)	7.72	0.01	3.83	0.12
s(D:ACI)	4.28	0.01	3.07	<0.01
s(D:DSH)	5.09	0.19	5.89	0.01
s(D:BOG)	1.00	0.88	8.45	<0.01
s(E, N)	25.39	<0.01	-	-

Table 4.15: Results of the two chosen all-habitat additive models fitted for the seven habitats: with and without Easting and Northing respectively. Where the covariate is a fitted as a smoothing spline, the estimate is of the degrees of freedom for that spline. The habitats abbreviations are as follows: BMY: Broadleaved, Mixed and Yew Woodland, CON: Coniferous Woodland, IGR: Improved Grassland, NEU: Neutral Grassland, ACI: Acid Grassland, DSH: Dwarf Shrub Heath and BOG: Bog.

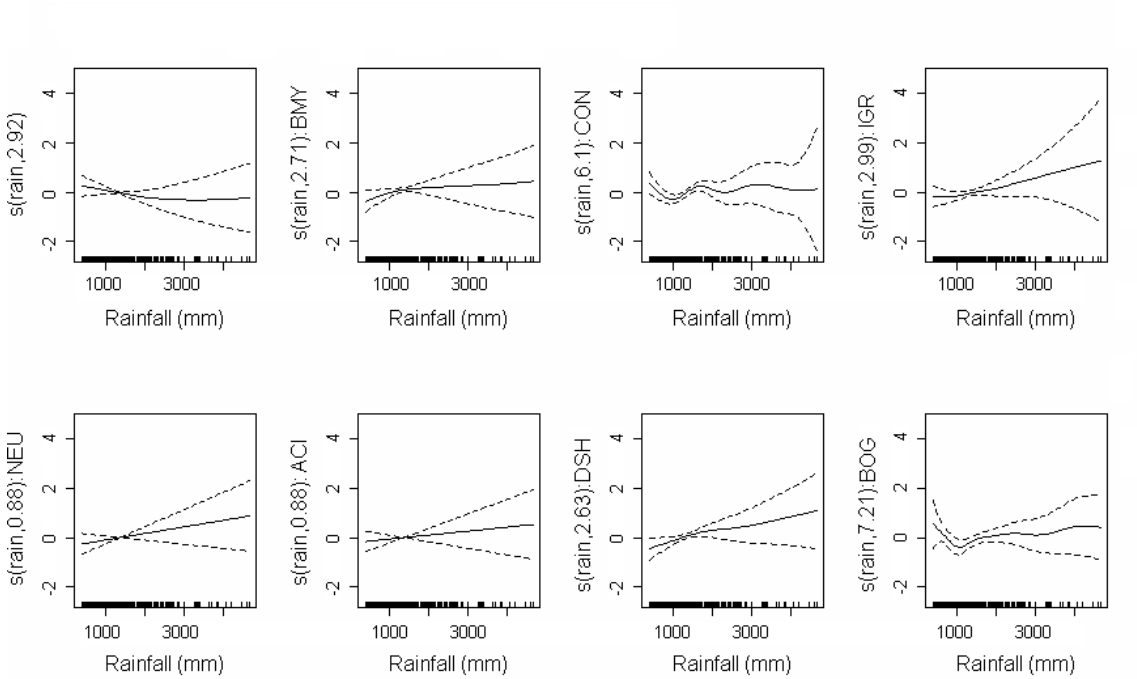

Figure 4.13: Smoothing splines for rainfall from the all-habitat AM with Shannon index response. Model covariates: s(D)+s(D:BH)+s(R)+s(R:BH)+s(E,N)+BH+Y.

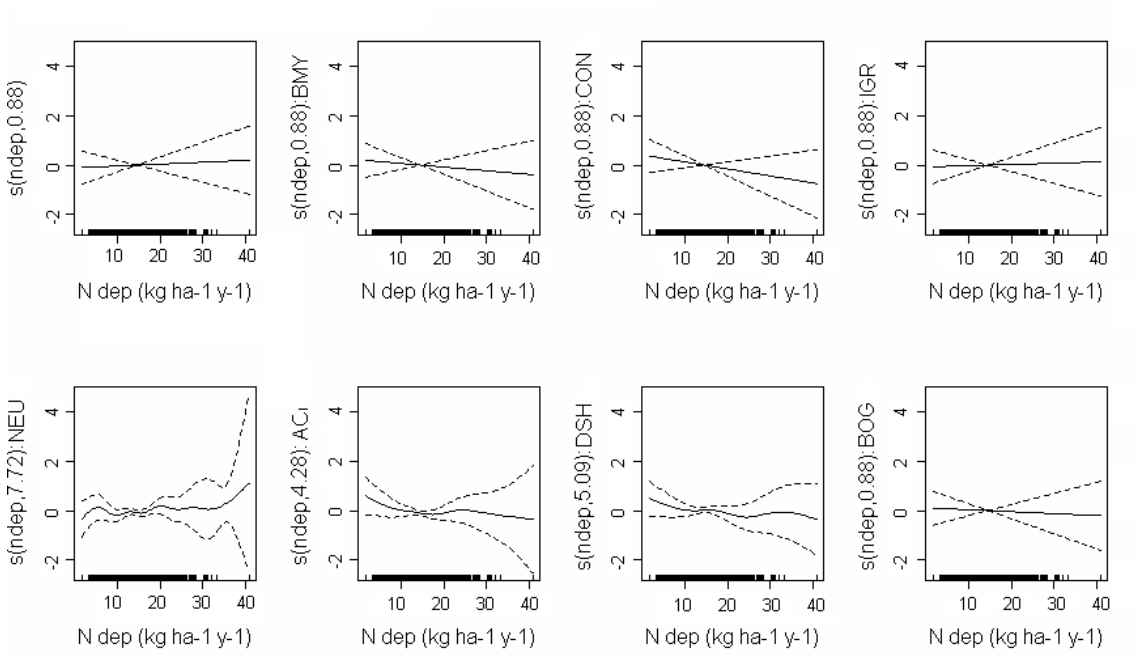

Figure 4.14: This graph shows the smoothing splines for nitrogen deposition from the all-habitat AM with Shannon index response. Model covariates: s(D)+s(D:BH)+s(R)+s(R:BH)+s(E,N)+BH+Y.

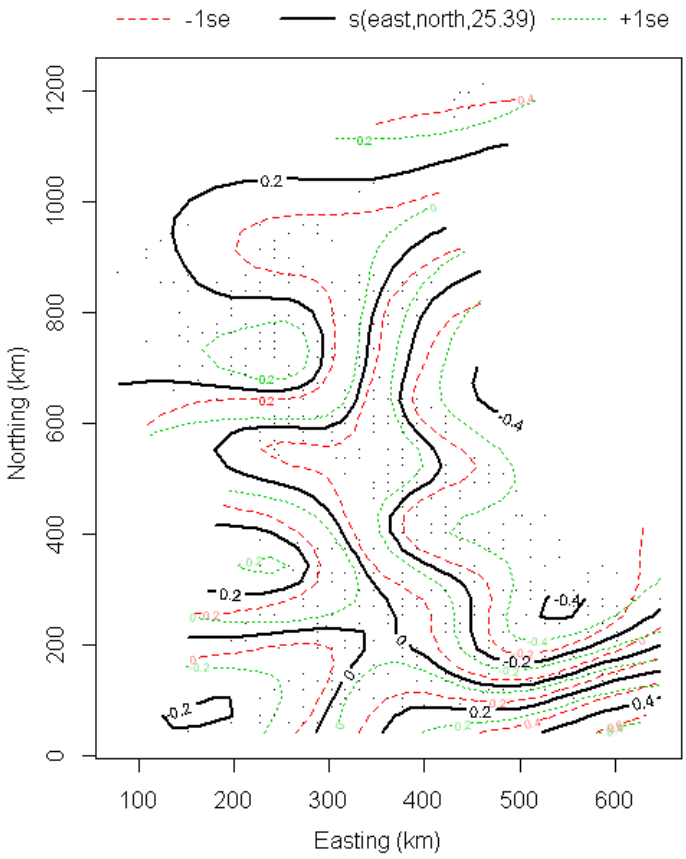

Figure 4.15: Graph of the joint smoothing spline for Easting and Northing from the final all-habitat Shannon index additive model.

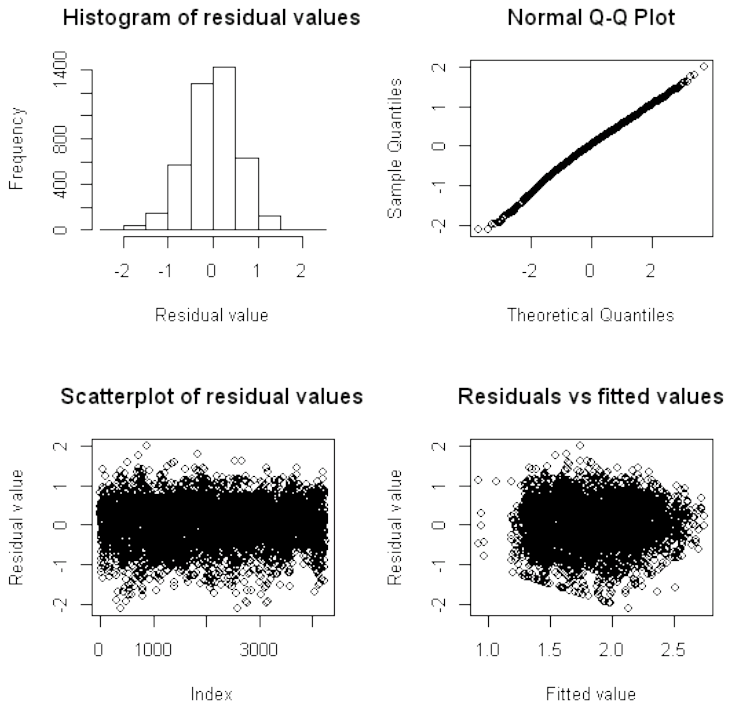

Figure 4.16: Diagnostic plots for the final all-habitat Shannon index additive model.

The resultant model in table 4.15 does not contain Altitude as a covariate; the interactive Rain:BH and Nitrogen:BH terms have been retained, allowing a better explanation of the deviance than in some previous models, in this case 26.4%. The joint smoothing spline for Easting and Northing has been retained and the covariate of year shows a small but highly significant effect, according to the analysis (Table 4.15). There is a very slight negative trend over time, of 0.002 index values per year. The estimated residual standard deviation is 0.56.

An overall spline for rainfall is fitted for all habitats as well as a spline for each Broad Habitat. This allows the overall relationship of the biodiversity response with rainfall and the habitat-specific relationships to be obtained. The smoothing splines for rainfall interaction with Broadleaved and Mixed Woodland (BMY) and Coniferous Forest (CON) are significant at the 5% level (Table 4.15, Figure 4.13).The former appears to be a mirror image of the slight positive relationship of the overall rainfall spline in the horizontal plane, indicating that the biodiversity in this habitat shows no trend with rainfall. The coniferous forest spline is clearly non-linear, and exhibits a nadir at around 1000 mm, and appearing fairly constant at rainfall levels above approximately 1500 mm.

The same fitting procedure is adopted for nitrogen deposition, with a spline fitted for all habitats as well as each individual habitat. The significant nitrogen deposition smoothing splines are for the Neutral (NEU) and Acid Grassland (ACI) habitats (Figure 4.14). The standard error bars on the other graphs are wide at either end of the splines, giving little help in identifying the relationship at the edges of the fitted range. As can be seen in figures 4.13 and 4.14, the trends for rainfall and nitrogen deposition are quite slight, where they are significant. The splines for the interaction terms of rainfall:Coniferous Woodland (Figure 4.13) and nitrogen:Neutral Grassland (Figure 4.14) appear to show particular signs of over-fitting; these estimated relationships may not be wholly ecologically realistic for sites where nitrogen is estimated to be greater than approximately 25 kilograms per hectare per year. Above this value, the number of sampling sites is too low to estimate the relationship between nitrogen deposition and the biodiversity response precisely; the standard error bars are also particularly wide apart for these values. The standard error bars for the interaction terms fitted as linear trends are due to the term being fitted as a spline in the model. The East-North smoother (Figure 4.15) has a gradient similar to that in the Improved Grassland model (Figure 4.9), with nadirs in the South and East of the country and peak estimates in the North-West. Only 26.4% of the deviance is explained in this model; there is almost three-quarters of the variability which cannot be explained by the chosen model.

Model	Covariates	AICc	Dev. expl.
1: AM	s(E,N) + s(R) + s(D) + s(R:BH) + s(D:BH) + BH + Y	7287	26.4%
2: AM, no E,N	s(R) + s(D) + s(R:BH)+ s(D:BH) + BH + Y	7426	23.2%

Table 4.16: Final models of tested Additive Model structures: Model 1 is the initial structure; the initial model tested for model 2 did not include Easting and Northing as covariates.

In order to assess how much of the variability in the response can be explained without the spatial location data, the same chosen AM is fitted without the Easting-Northing smoother. The resultant model still explains almost a quarter of the model deviance, but the AICc value has increased greatly, indicating poorer model performance, given the parameters used to fit the model. (Table 4.16). Most of the covariates are similar to the AM with Easting and Northing; the degrees of freedom associated with each spline are similar in most cases (Table 4.15). Given this similarity, it appears as if the fitted spatial trend is not directly confounded with other covariates in the model. Also, the two-dimensional spatial smoother fitted only explains a small amount of extra deviance in the response data. This leads to the inference that biodiversity as described by the Shannon index is not affected by spatial position per se, but more by the environmental conditions present at that location, such as habitat or rainfall.

4.5.3 Additive Mixed Model

Variability within the CS sites is important to be estimated, in order to make inference on the variance between the sites and within the sites, between the plot responses. The Additive Mixed Model structure used in the following models is as follows:

$$y_i = \mathbf{X}_i\beta + s_1(x_{1i}) + s_2(x_{2i}, x_{3i}) + \cdots + \mathbf{Z}_i\mathbf{b} + \varepsilon_i, \tag{4.6}$$

which is similar to the AM structure in equation 4.1, with the addition of random effects. In the above equation $\mathbf{Z}_i$ is the ith row of the random effects matrix and $\mathbf{b}$ is the vector of coefficient estimates, where $\mathbf{b} \sim N(0,)$ The error terms, ε_i, are distributed as $\varepsilon_i \sim N\left(0, \sigma_\varepsilon^2\right)$. The model tested will then be:

$$S_{ikl} = s_1(E_i, N_i) + s_2(A_i) + s_3(R_{il}) + s_4(R_{il} : BH_{ik}) + s_5(D_i) + s_6(D_i : BH_{ikl}) + \beta_1 BH_{ikl} + \beta_2 Y_l + \beta_3 + \mathbf{Z}_i \quad (4.7)$$

The Additive Mixed Model structure, as outlined in equation 4.6, will be used for the model of the seven habitats, in much the same way as for the AM setup. Random effects will be used here to look at the "within CS site" variability. This is valuable in understanding how biodiversity varies over the small 1km region. As the plots themselves are randomly located within the 1km region, we can interpret their locations as being randomly distributed with the site.

An example of how the model selection process is conducted is shown below. A complex covariance structure for the residual error values has not been imposed upon the model, so in this case the residuals $\varepsilon_i \sim N(0, \sigma^2)$, where σ^2 is assumed to be constant. The Additive Mixed Model is fit using Maximum Likelihood (ML) and the final model is selected via the backward selection process and the AICc value as sole criterion. In order to obtain unbiased estimates of the variance parameters, the final model is refitted using Restricted Maximum Likelihood (REML; Table 4.17).

Covariate	Estimate	Std. Error	P-value
BMY	2.11	0.04	<0.01
CON	1.84	0.04	<0.01
IGR	1.66	0.02	<0.01
NEU	2.09	0.03	<0.01
ACI	2.08	0.04	<0.01
DSH	1.90	0.04	<0.01
BOG	1.96	0.04	<0.01
Rain (mm)	7.50×10^{-5}	3.25×10^{-5}	0.02
Year	-0.002	0.001	0.02

Model effect	Est. d.f.	P-value
s(E, N)	13.25	<0.01

Random effects	Est. S.D.
Site	0.53
Residual	0.23

Table 4.17: Results of the selected AMM fitted for the seven habitats. Where the covariate is a smoothing spline as indicated by $s(\cdot)$, the estimate is of the degrees of freedom for that spline. The estimated standard deviations of the random effects are also given below.

Models without environmental covariates				
Model	Covariates	Between Site	Within Site	Dev. expl.
AM	s(E, N)+Y	-	-	13.1%
AMM	s(E, N)+Y	0.29	0.54	12.2%
Models selected with AICc				
Model	Covariates	Between Site	Within Site	Dev. expl.
AM	s(E, N)+s(R)+s(D)+s(R:BH)+s(D:BH)+BH+Y	-	-	24.5%
AMM	s(E, N)+R+BH+Y	0.23	0.53	21.4%

Table 4.18: Model results for the chosen additive and additive mixed models for the Countryside Survey all-habitat Shannon index model. The mixed model has Site as a random effect. The '*' symbol indicates a multiplicative effect; ':' indicates an interactive effect. AM: Additive Model, AMM: Additive Mixed Model. Covariates are E: Easting, N: Northing, R: Rainfall, BH: Broad Habitat, D: Nitrogen deposition. The "Between site" and "Within site" standard deviations are shown, as well as the deviance explained. Models fitted only with a spatial smoother for the two surveys, with and without random effects are also summarised. These models were only fitted with the joint Easting and Northing smoother. The deviance explained in each case is calculated relative to the residual deviance of the null model, which has a mean component fitted and same random effects structure as the respective tested models.

Comparing the results of the AMM (Table 4.17) and the model without random effects in place (table 4.15), the AICc value is slightly reduced (Table 4.18). Also, the residual standard deviation is estimated to be slightly lower at 0.51 (2 d.p), compared with a value of 0.56 in the model without random effects. The between and within-site standard deviations are estimated to be 0.19 and 0.50 respectively. This indicates that there is a large amount of variability at the sub-site level, which cannot be explained by the environmental covariates. The diagnostic plots show no reason to infer violation of the model assumptions (Figure 4.17). Apart from habitat type and previous survey index, there is no variation available in the explanatory variables to account for this fine-scale variability. The variation between responses in each plot can only be explained by these environmental factors.

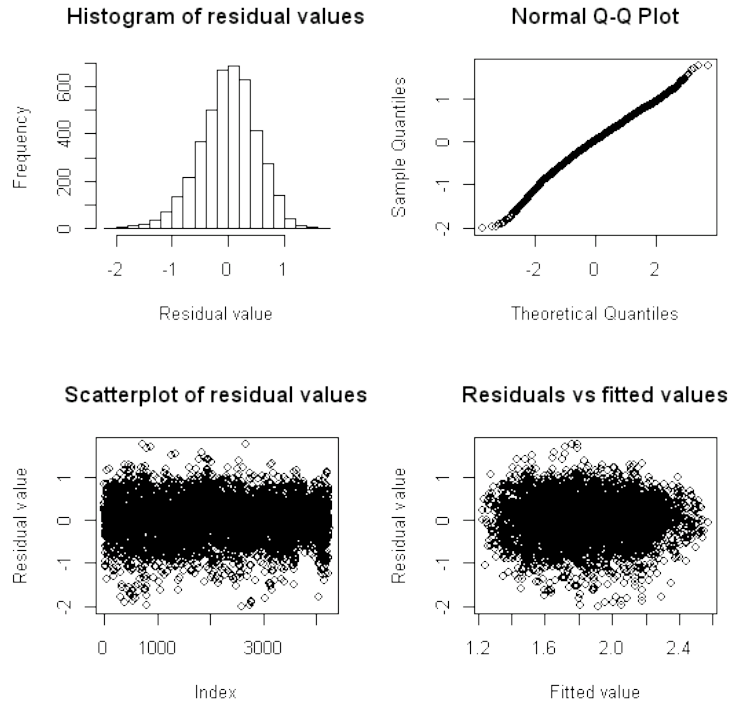

Figure 4.17: Diagnostic plots of the Countryside Survey all-habitat Shannon index model with random effects.

Further to modelling the response of the three latest CS results together, models of individual surveys will now be fitted, in order to see how the biodiversity in one survey is related to the biodiversity at the same site in the next survey.

4.5.4 Single year surveys

The reason for creating a model with only a single survey as the response is to examine more specfically how the environmental factors spatial differences in biodiversity for a more restricted period of time. In comparison to the models in this chapter up to this point, the 1998 and 2007 data are modelled separately. The resultant models will then be compared. Nitrogen deposition and rainfall are put into the initial model, as interaction terms with the categorical covariate Broad Habitat. Thus, the relationship between the response and these covariates can vary, depending upon the Broad Habitat in which the response is measured.

In the previous multi-survey models, the state of the relationship between covariates, such as rainfall or Nitrogen deposition, and the biodiversity response was not allowed to vary temporally. It is assumed that the relationship between each covariate and the model response is the same at all points in time; i.e. for all surveys. It is possible that the magnitude or significance of such relationships would have the capacity to differ greatly between surveys. Thus, single survey models help to show a more precise relationship between model covariates and each survey's response, giving a better understanding of which the biodiversity at a point in time can be best described by certain covariates.

In choosing to look only at the plots from a single survey, plots that were surveyed in consecutive surveys are needed. The 1984 survey was smaller in remit than the other four CS surveys, due to a lack of funding. Consecutive surveys for consideration are the 1990, 1998 and 2007 surveys, with 1998 and 2007 to be used as responses in separate models and the data from 1990 and 1998 to be used as respective covariates. Given that the previous survey index is used as a covariate in these models, the response effectively is the change in the biodiversity since the previous survey, described in terms of the previously used environmental covariates. It is predicted that the previous biodiversity index value will have a large influence on biodiversity at a future point in time. Thus, the other additive covariate contributions will explain that effect which is not described by the previous value. The periods between these surveys are 8 and 9 years respectively, so the time between these surveys is roughly similar.

Both an Additive Model and a Additive Mixed Model are to be fitted for each survey. In the Additive Mixed Model setup, the factor of CS 1km site is included as a random effect. Models are chosen by backward selection, again using the criterion of the model AICc. The initial fixed effects in each case were as follows:

$$S_{ik} = s_1(E_i,\, N_i) + s_2(A_i) + s_3(R_i) + s_4(R_i : BH_{ik}) + s_5(D) + s_6(D_i : BH_{ik}) + \beta_1 BH_{ik} + \beta_2 + \varepsilon_{ik} \tag{4.8}$$

Here, S_{ik} is the Shannon index response at plot j in site i, E_{ij} and N_{ij} are the Easting and Northing position values and A_i, R_i and D_i denote the regional mean altitude, rainfall estimates and Nitrogen deposition estimates respectively. $\mathbf{beta}_1$ is the vector of Broad Habitat coefficients and β_2 is the intercept

1998 AM			
Covariate	Coef. est.	Std. Error	P-value
BMY	2.12	0.06	<0.01
CON	1.95	0.09	<0.01
IGR	1.62	0.04	<0.01
NEU	2.03	0.06	<0.01
ACI	2.24	0.08	<0.01
DSH	1.75	0.06	<0.01
BOG	1.97	0.06	<0.01
Covariate	Est. d.f.		P-value
s(E, N)	22.09		<0.01
s(R)	1.00		0.61
s(R:BMY)	1.00		0.65
s(R:CON)	7.08		<0.01
s(R:IGR)	1.00		0.61
s(R:NEU)	1.00		0.63
s(R:ACI)	3.10		0.03
s(R:DSH)	1.00		0.87
s(R:BOG)	1.00		0.69
s(D)	1.00		0.94
s(D:BMY)	1.00		0.42
s(D:CON)	1.43		0.16
s(D:IGR)	1.00		0.30
s(D:NEU)	1.44		0.04
s(D:ACI)	3.43		0.51
s(D:DSH)	1.00		0.58
s(D:BOG)	1.00		0.87

Table 4.19: Model parameter estimates for the single survey AM for 1998.

1998 AMM			
Covariate	Coef. est.	Std. Error	P-value
BMY	2.39	0.14	<0.01
CON	2.17	0.36	<0.01
IGR	1.43	0.10	<0.01
NEU	1.66	0.14	<0.01
ACI	2.18	0.17	<0.01
DSH	1.94	0.14	<0.01
BOG	1.99	0.14	<0.01
D:BMY	-0.02	0.009	0.02
D:CON	-0.02	0.008	<0.01
D:IGR	0.02	0.007	0.01
D:NEU	0.02	0.008	<0.01
D:ACI	-2.4	0.009	0.79
D:DSH	-0.10	0.008	0.26
D:BOG	-0.02	0.009	0.99
Covariate	Est. d.f.		P-value
s(E, N)	11.83		<0.01

Table 4.20: Model parameter estimates for the single survey AMM for 1998.

The chosen fitted models for the AM and AMM 1998 survey models are laid out in tables 4.19 and 4.20. In comparison with the model using all three survey values as the response (Tables 4.15, 4.17), the results are quite similar. For the 1998 AM structure, most of the smoothing splines have lower degrees of freedom than for the model of all three surveys. The splines for the Coniferous Woodland (CON) habitat are more complex however. The bivariate smoother for Easting and Northing is simpler in both 1998 models. As shown in table 4.21, the chosen 2007 AM and AMM did not include rainfall or nitrogen deposition in the chosen model. The diagnostic plots for the four selected models show no major violation of model assumptions in any case (Tables 4.18 - 4.21).

Models without environmental covariates				
Model	Covariates	Between site S.D.	Within site S.D.	Dev. expl.
98 AM	s(E,N)	-	-	17.6%
98 AMM	s(E,N)	0.32	0.47	15.8%
07 AM	s(E,N)	-	-	14.4%
07 AMM	s(E,N)	0.22	0.59	13.7%
Models selected according to AICc				
Model	Covariates	Between site S.D.	Within site S.D.	Dev. expl.
98 AM	s(E,N) + s(R) + s(R:BH) + s(D) + s(D:BH) + BH	-	-	30.9%
98 AMM	s(E,N) + D*BH	0.28	0.45	25.5%
07 AM	s(E,N) + BH	-	-	20.1%
07 AMM	s(E,N) + BH	0.19	0.58	19.4%

Table 4.21: Results of the single survey models, for 1998 and 2007, with and without random effects. The mixed model has Site as a random effect. The '*' symbol indicates a multiplicative effect; ':' indicates an interactive effect. AM: Additive Model, AMM: Additive Mixed Model. Covariates are E: Easting, N: Northing, R: Rainfall, BH: Broad Habitat, D: Nitrogen deposition. The "Between site" and "Within site" standard deviations are shown, as well as the deviance explained. Models fitted only with a spatial smoother for the two surveys, with and without random effects are also summarised. These models were only fitted with the joint Easting and Northing smoother. The deviances explained are calculated relative to the null models, which have a mean component and sole fixed effect and the same random effect structure as the models against which they are tested.

The percentages of deviance explained by the 1998 models for both the AM and AMM are much greater than the respective models with only an Easting and Northing spline fitted, which only explain about one third of the deviance in the null model (Table 4.21). However there is still over two thirds of the deviance unexplained in the 1998 selected models. The 2007 models show less explanatory power, as the AICc-selected models explain around 20% of the deviance. As can be seen, the random effect standard deviations are not greatly reduced in the AICc selected models. The within-site varibility for the selected AMMs is much larger than the variability between sites. This concurs with the results in table 4.18, where the selected AMM for data from all three surveys shows a large amount of variability between plots within sites.

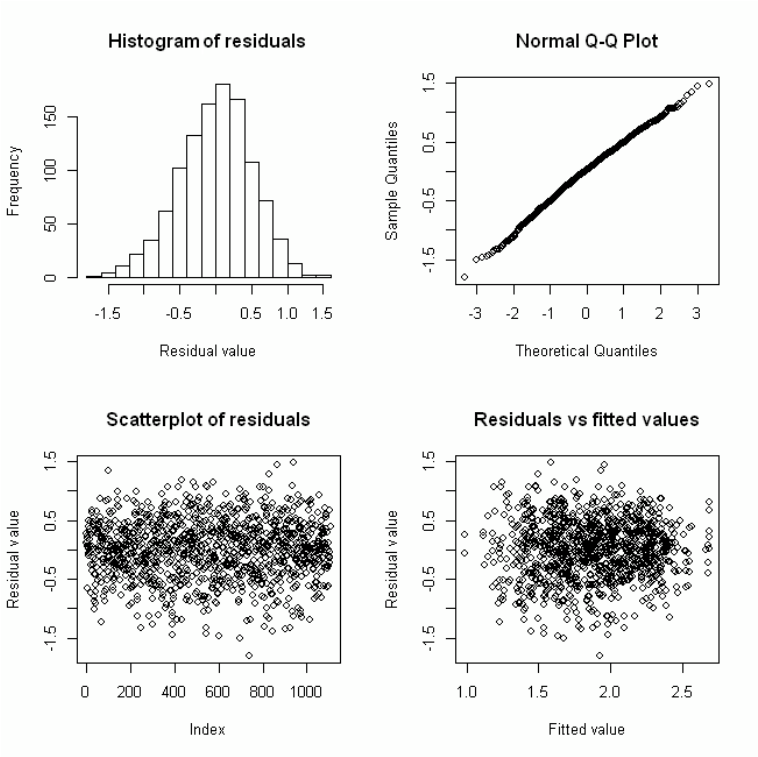

Figure 4.18: Diagnostic plots for the chosen 1998 survey AM.

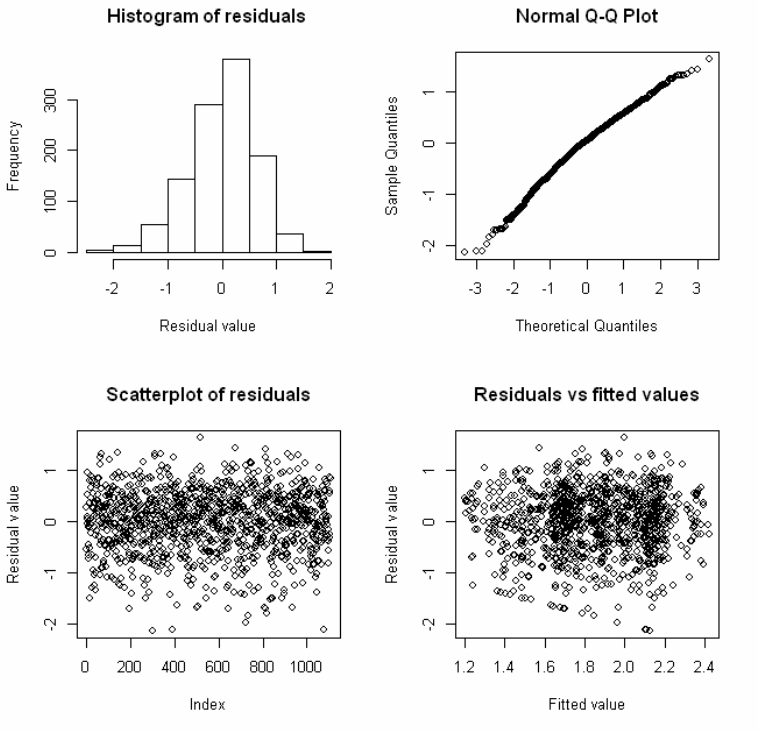

Figure 4.19: Diagnostic plots for the chosen 2007 survey AM.

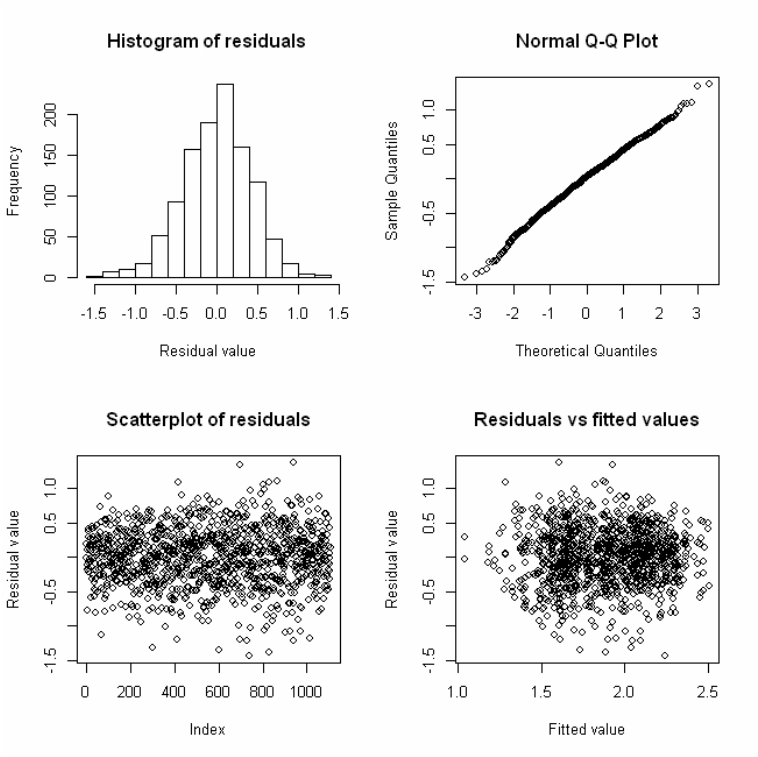

Figure 4.20: Diagnostic plots for the chosen 1998 survey AMM.

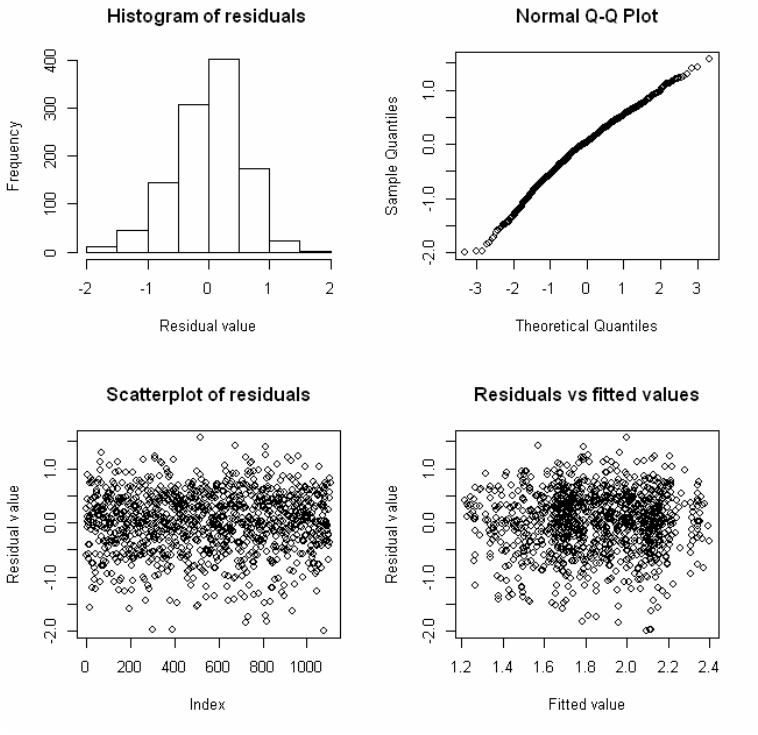

Figure 4.21: Diagnostic plots for the chosen 2007 survey AMM.

Comparison of models

All the final models detailed in table 4.21 include a joint spline for Easting (E) and Northing (N). Broad Habitat (BH) is also included as a fixed effect in all models. The 1998 models both include the rainfall (R) and nitrogen deposition (D) covariates, both as interaction terms with Broad Habitat in differing forms: with splines fitted in the Additive model structure and as linear covariates in the mixed model. With regard to the comparison with the models in table 4.21, the residual deviance is lower in the AICc-selected models; the 1998 models have relatively greater explanatory power. The 2007 models only include the Easting and Northing spline and the Broad Habitat categorical covariate; the deviance explained, at just below 20%, is much lower than for the 1998 models.

4.6 Discussion

The aim of this chapter was to analyse the Countryside Survey data with regard to temporal and spatial changes in biodiversity at randomly positioned plots in semi-rural habitats. Possible environmental drivers and pressures of change were used as model covariates in order to describe the change in biodiversity in a generalised additive model structure.

The initial models used the biodiversity results of the three most recent CS surveys as the response data. The arable habitat plots were removed from the dataset, due to the prevalence of land management having a large effect on the response at these sites and their subsequent poor fit in the individual habitat models. The resultant models show rainfall interaction with Broad Habitat to have a statistically significant relationship with the biodiversity responses, particularly for the Coniferous Forest and Acid Grassland habitats. Both show non-linear relationships, which are not necessarily result of rainfall. Further investigation into this reasons for these effects is necessary. Nitrogen deposition is also included as a significant covariate; the splines obtained for its Neutral Grassland, Acid Grassland and Dwarf Shrub Heath in figure 4.14 show signs of over-fitting, indicating that more detailed specific analysis of the data is needed to understand the relationships fitted in this model. The removal of the easting and northing covariates did not reveal any different relationships that were not present with their inclusion in the model.

The single survey models were fitted to analyse the trends in biodiversity for a defined period, i.e. that of the survey. These models for the 1998 and 2007 survey data respectively produced differing results, with the 1998 models explaining a larger percentage of deviance explained by the covariates (Table 4.21). In both the Additive and Additive Mixed Models for the 1998 data, both rainfall and nitrogen deposition were included as interaction terms with Broad Habitat. The additive mixed model fitted for the 1998 CS data in table 4.20 showed differing relationships by Broad Habitat between biodiversity and nitrogen deposition. While the biodiversity index in Improved and Neutral Grassland showed a slight but significantly positive response to nitrogen, in the Acid Grassland there was a large negative but non-significant effect. The Neutral Grassland effect could be that ruderal species which can take advantage of higher nitrogen deposition increase the Shannon index in that habitat. In the Broadleaved, Mixed and Yew Woodland, Coniferous Forest, the negative coefficients are small but significant.

Although the Shannon index was used as the main response in these models, there was positive correlation between species richness and the Shannon index across all plots in the dataset. As a result of this, it is surprising that the same relationship between nitrogen deposition and the univariate biodiversity measure of interest here does not cohere more precisely with previous research highlighted earlier in this chapter (Maskell et al., 2010). Closer analysis of these effects in individual habitats would be needed to check the influence of sites with extreme deposition values associated with them, as performed by Stevens et al. (2004). In the 2007 model, neither of these covariates were included. More information on the nitrogen deposition over time and the temporal trend in rainfall over the period prior to a survey being conducted may help in relating this spatial variability to the changes in the covariates.

Given that there is a substantial percentage of deviance unexplained in the GAMs fitted in this chapter, there could be other environmental covariates in many locations causing large variation in the biodiversity response. These could be anthropogenic changes, linked to nutrient loading or disturbance or other local land use, causing deposition of nitrogen compounds, for instance. Such effects are not recorded, nor can they be deduced from gridded values.Year was not fitted as a random effect in the analysis. Given only three survey were used in the analysis, the estimation of the variation between survey years would be subject to great uncertainty.

Biodiversity as a response to environmental covariates should not be inferred solely by reference to changes within the plant community dynamic, or from relationships with covariates

which may have local uncertainty associated with them. Re-prediction of the covariates and estimation of this fine-scale uncertainty can help in the assessment of the effect of these environmental drivers and pressures and analysis of relationships with downscaled covariates. With regard to the DPSIR framework, care must be taken when ascribing an observed impact in the environment to drivers and pressures which have associated uncertainty which is not accounted for.

Having selected an additive model for the 1998 survey which includes both rainfall and nitrogen deposition, an important issue to study is that of covariate uncertainty. As has been discussed in the analysis results, there is a large proportion of variability at the sub-site level, as indicated by the fitted AMMs (Table 4.21). Apart from Broad Habitat, there is no environmental covariate data in the model which varies at the sub-site level. The rainfall and nitrogen deposition values were estimated at the 5km and 1km grid levels respectively. The given values are used as covariates for the sampling sites co-located with the grid cells. As such, they are taken to be representative of the value of the environmental covariate at the position of the response. However only point estimate values of the gridded rainfall and nitrogen data are used, so no information on the intra-square variability is available.

The within-site variability would not be present, if there were a uniform response to the rainfall and nitrogen covariates for each Broad Habitat. Thus, the Broad Habitat-specific spline for the environmental covariates would the variability in the response exactly. There is therefore residual variability within the 1 km CS sites which was not able to be explained by the selected models. In order to improve the model performance, the fine-scale uncertainty in these covariates will be estimated as part of a hierarchical model structure, allowing the intra-square variability to be incorporated into the model, and assessment made as to the impact of these covariates, given the estimation of their local uncertainty. The covariate data should be realigned to the position of the biodiversity responses, which are available at a finer-scale.

A generalised additive model structure has been used to model variability in plant biodiversity with rainfall and nitrogen deposition in particular as covariates in the tested models. Relationships between these covariates and the biodiversity response have been observed. However, CS plot data are recorded at a finer scale than both rainfall and nitrogen deposition. Variability at the plot level is not available and could be important in estimating the

relationships between the covariates and the response.

$\sim$

Chapter 5

Data realignment

This chapter explores a possible downscaling methodology to realign an environmental covariate at a relatively coarse scale to the fine-scale level of the response in a regression model. In chapter 4, the possibility of realigning the rainfall and nitrogen deposition grid square measurements to the CS plot level was proposed, but relationships were not strong enough in order to show the effectiveness of the procedure. A simulation is constructed in order to downscale a covariate and fit the biodiversity response against the realigned values. The resultant models is recorded and assessed with regard to the variability of the covariate at coarse and fine scales.

The realignment method will be conducted using altitude measurements and gridded rainfall data in the vicinity of the CS sites in order to downscale the rainfall values. The simulated dataset is structured in the same way as the Countryside Survey (CS) dataset in chapter 4. The simulation uses rainfall as the sole covariate in a linear model, in order to help the subsequent effects on the model inference and how strong the correlation between rainfall and altitude is required to be, in order to warrant the downscaling of gridded covariates in this manner.

5.1 Introduction

A challenge present in the structure of the data presented in the chapter 4 is the differing scales of the model covariates and response data. Given that some of the explanatory covariates in the model are estimated over much larger regions than those at which the response data are collected, what relationships may be occurring in the environment between the covariates and response are lost within these large differences in scale between what is estimated to be occurring at the 1 and 5 kilometre grid square levels, and what is potentially occurring at ground level, at the Countryside Survey 200m^2 plot-level. Errors incurred within these differences in scale can create false trends (or invalidate true relationships) in the models (Carroll, 2005; Armstrong, 1998; Yanez et al., 1998). Also, due to the randomly located plots within each Countryside Survey 1 km square, the positions to which the covariate data is to be realigned, do not sit on a regular grid. Thus, a method is needed to realign the data and re-estimate covariates of interest at the response scale level while taking account of the uncertainty in those estimates.

5.1.1 Importance of covariate realignment

Rainfall in Great Britain has large local-scale variability; rainfall levels between two nearby locations can vary greatly. Fine-scale variation in rainfall is associated with topographic effects, such as aspect, gradient and altitude. Rainfall is positively correlated with altitude in Great Britain (Brunsdon et al., 2001). This effect is sometimes described as topographic enhancement. McClatchey (1996) explores the relationship between altitude and rainfall in different regions in the Scottish Highlands, finding a generally positive relationship between altitude and rainfall, with variation in the strength of this relationship between regions. Higher rainfall is expected on slopes facing the prevailing wind direction, as they are more open to precipitation. Likewise, slopes facing the other way are more sheltered and so less rainfall would be expected over the course of a year at these locations. Where the terrain varies within a local region, variability in rainfall would also be expected to vary with altitude, given that the prevailing wind during rainfall could come from any direction, and precipitate more upon the slopes facing the wind at that time.

In the analysis in chapter 4, the rainfall covariate has been estimated at the 5km grid square level. However rainfall can be highly variable within a 25km^2 region: Bitew and Gebremichael (2010) show the high daily variability in rainfall at the across a 36km^2 km grid in

mountainous terrain, using rain gauges in each kilometre square. The coefficient of variation within the sampled region for single days with heavy rainfall varied between 15 and 53%, with an average of 25%. Although these data were collected in the Ethiopian Highlands in a period of high precipitation, it is an example of the potential for large variation in rainfall values within a small region comparable in size with the grid squares used in this analysis. Also, the coefficient of variation was estimated for single days; over a much longer period such as a year, the size of the variation cannot be directly extrapolated. It could increase over the year or extreme events could even out due to changes in wind direction. Studies such as this are very labour-intensive, and are not conducted often.

The nitrogen grid estimates are based on model results, as described by Smith and Fowler (2001) and Smith et al. (2000). Nitrogen deposition is estimated at a finer scale than rainfall, with estimates of total deposition at the 1km grid level. Experiments of the effect of poultry farms on the local environment show that the majority of ammonia emissions tend to be deposited within a few hundred metres of the emission site (Theobald et al., 2004). In order to include these identified sources of nitrogen emissions in the downscaling procedure, the locations of the sites would be needed. Information on the precise locations of these sites are undisclosed, and so cannot be accommodated into the nitrogen deposition estimates downscaling process.

In discussing the spatial variability of atmospheric ammonia, Sutton et al. (1998) state that due to the integration of agricultural land and semi-natural areas in the United Kingdom, high spatial variability of ammonia in these regions is typical; the impact of a single source decreases approximately exponentially with distance from the emission location, dependent upon meteorological conditions and landscape. In a study conducted on the spatial impact of ammonia emissions from poultry farms, Pitcairn et al. (2002) estimated the total nitrogen deposition downwind of the livestock buildings to vary greatly within a small spatial area. At 30 m distance from the buildings, nitrogen deposition is estimated to be 80 kg ha^{-1} $year^{-1}$, decreasing to 14 kg ha^{-1} $year^{-1}$ at a distance of 650 m. Uncertainty of dry nitrogen deposition value means that a point estimate within a 1km region does not take account of the potential variation in the grid square, due to the high variation around point sources. In remote upland areas, it is assumed that wet nitrogen deposition dominates the total nitrogen deposition, and as a result is greatly dependent upon rainfall levels (Sutton et al., 1998). Due to many of the CS sites being located close to agricultural land, it is expected that the difference between the 1km grid square estimates and the true nitrogen deposition will be highly variable.

Very little information is available on the within-square uncertainty of the CBED nitrogen deposition data, partly since deposition is only measured at a few sites across the United Kingdom (Matejko et al., 2009) and assessment of the very local uncertainty would be very difficult and costly. Smith et al. (2000) concede there is considerable error in nitrogen deposition grid square estimates. Dore et al. (2006) note that the uncertainty of input parameters for FRAME (Fine Resolution Atmospheric Multi-pollutant Exchange) deposition maps of the United Kingdom is not completely understood. A sensitivity analysis would be very complex, requiring the variation of multiple parameters. Such an analysis has thus far not been attempted, although suggestions for possible methods have been proposed (Dore et al., 2006; Oxley and ApSimon, 2011). The error involved in the composition of the rainfall data is not known, as the data are produced by the Met. Office and the model used is not publicly available.

Information on covariate sub-grid variability would be very useful in understanding the theme of covariate uncertainty. However, the issue remains of precisely identifying the value of the covariates at the plot level. Due to the high variability of rainfall and nitrogen deposition at the subgrid level, this could affect model performance when modelling biodiversity at the plot level using these environmental covariates at such coarse spatial scales. Therefore it is important to estimate the respective covariates at the CS plot level more precisely, as well as take account of the uncertainty associated with these re-predictions. It is widely known that rainfall is correlated with altitude at small scales; Daly et al. (1994) state this effect and take advantage of this effect in predicting rainfall, by assuming that the local relationship is linear. In upland areas, where elevation is more variable, nitrogen deposition is dominated by wet deposition, as previously stated, and thus positively correlated with altitude in such regions.

In the previous models in this thesis, estimates of rainfall for the year in which the survey was conducted are used, with the estimated rainfall values assigned to all plot in their associated grid squares in chapter 4 or as measurements for all transects at that site in chapter 3. This philosophy was assumed in the models fitted in this thesis up to this point. The temporal and spatial misalignment of covariates and their respective responses was not corrected and the covariate values were assumed to be appropriate surrogates of the true value at the scale of the response. This simplistic assignment follows the methodology of the Thiessen polygon for the plant data.

When data are already considered available on a regular grid, the implementation of the Thiessen polygon is trivial and thus the na¨ıve method of downscaling is to assume that the variable given at the coarse-scale is uniformly distributed across each region for which it is estimated. With such environmental covariates as rainfall, it is not believed that its distribution is so discrete across a gridded region, but the assumption is made that the gridded data available are satisfactory without the attempt to estimate the point-level data more precisely. Given the information on rainfall distribution this may be too great an assumption to make in the analysis. However, the values for each grid square are estimated and have no associated error attached to them. This misalignment between covariate and response data will be addressed in this chapter and a method proposed for similar datasets, where no further information is directly available on the covariates which are to be downscaled than the gridded model output.

The aim of realigning the covariates is two-fold: firstly to more accurately estimate the rainfall and nitrogen deposition at the location of each CS plot, rather than using the grid square value; secondly to take account of the uncertainty associated with each newly estimated value. The fulfilment of these aims are necessary in order that correct inferences are made as to the relationships between these explanatory covariates and the biodiversity responses.

5.1.2 Downscaling methodologies

Downscaling refers to the estimation of a certain environmental covariate at a certain temporal and/or spatial scale, given the previous obtained values at a coarser scale. These obtained values may themselves have been directly measured or modelled over a defined region.

A more developed approach might be to assume that the gridded rainfall data, for instance are actually point data for the centroid of each grid square for which they are defined. One can then interpolate this grid of points by assuming that rainfall varies linearly between all gridded values. In this way, a point estimate can be defined for the complete region of interest. This approach to misalignment is relatively simplistic, that environmental covariates vary linearly between the given point values.

A comparison of different methods to interpolate rainfall is made by Goovaerts (2000), by assessing the ability of each method to accurately predict the rainfall measurements in Southern Portugal in the Algarve. Seven different interpolation procedures are presented; the inclusion of elevation data in predicting monthly rainfall levels is in three of these methods. The performance of each method is assessed using cross validation of the predictions with known values. The first method is the Thiessen polygon (Thiessen and Alter, 1911), where a location with unknown value is ascribed the value of the nearest weather station.

Inverse Distance Weighting (IDW) is where the value of rainfall predicted at a certain point is the mean of those sites closest to it, where the weighting ascribed to each site is inversely proportional to the square of the distance between the site with known value and the site to be predicted. The value of the variable of interest at an unmeasured location $\mathbf{s}_0$, is estimated to be the sum of N weighted nearby locations within a given distance of $\mathbf{s}_0$:

$$\hat{Z}(\mathbf{s}_0) = \sum_{i=1}^{N} \lambda_i Z(\mathbf{s}_i) \tag{5.1}$$

where the λ_i are the respective weights for each measurement i and $\lambda_i = \frac{c}{d^p N}$ where $d =$

$|\mathbf{s}_0 - \mathbf{s}_i|$ and the choice of the constant p affects how steeply the effect of the surrounding measurements decline with the distance from the location to be estimated. A larger p will increase the steepness of the decline. The constant c is chosen such that $\sum_{i=1}^{N} \lambda_i = 1$.

Kriging is similar in philosophy to IDW, in that the value of the covariate of interest at an unmeasured site is calculated according to equation 5.1, but the λ_i are obtained by the correlation structure of the random variable, Z over the region of interest. The λ_i are chosen such that the variance of Z is minimised.

Kriging, which assumes a spatial correlation between sites closer to one another, is tested by Goovaerts (2000) using three different variants. The predicted rainfall values at unsampled locations are estimated to be a linear combination of the neighbouring sites. In each method, the estimated correlation between observations is used to predict the rainfall at new sites, such that the estimation variance is minimised and the prediction values are unbiased.

Simple Kriging with local means (SKlm), Kriging with External Drift and Cokriging are the three methods tested. Sklm involves the regression relationship between rainfall and

elevation, which allows the local mean of rainfall to vary spatially. Kriging with external drift uses SKlm to derive local means, then simple kriging is performed on the residuals of the regression relationship. Cokriging is a multivariate extension of Kriging, whereby elevation and rainfall spatial correlations are estimated together, in order to predict rainfall at new sites.

In this example study by Goovaerts (2000), Kriging is noted to be advantageous for sparser, less dense networks, and SKlm has the lowest mean squared error of the three methods, whereas Cokriging has the highest mean squared error. Linear Regression as a method of interpolation, as also tested by Goovaerts (2000), involves estimating a regression of rainfall on elevation, which can then be used to predict rainfall, given the known elevation at a new location. The usefulness of linear regression as a method is advised in preference to ordinary kriging when the correlation between rainfall and elevation is at least 0.75.

Another possible method to use in downscaling is Perfect prognosis. This method was developed with the aim of using Global Circulation Models to estimate data at the regional level. It is a form of statistical downscaling developed by Klein (1971) as part of a precipitation forecasting method; the generic method is described by Maraun et al. (2010). It is a method for downscaling a certain model covariate by regressing it against other predictor variables known at the same locations and timepoints. The value of the response covariate, the predictand, can then be predicted for new values of the predictor variables against which is was regressed and also taking into account the error term. The underlying assumption in this method is that those relationships which are estimated at one spatial-temporal scale also hold at the scale, period or region of interest for which the predictand is desired to be known. The relationship estimated between predictand and predictor(s) could be a regression, making the method similar in methodology to the linear regression. However, the regression relationship can be flexible over the region of interest.

Predictor covariates used in the downscaling of precipitation in various models have been summarised by Wilby and Wigley (2000). A large number of different meteorological effects have been used, including air pressure, vorticity, mean sea-level pressure, wind direction, cloud cover, altitude, distance from the coast the North Atlantic Oscillation index and humidity. Modelling strategies used in the downscaling process are also varied: multivariate analyses, regression model, artificial neural networks and stochastic and semi-stochastic techniques have all been employed.

Fuentes and Raftery (2005) develop a method for the interpolation of spatial data incorporating observed data and areal block data at different resolutions. The data used in this context are dry deposition data in the United States. The observed data are from an irregular network of measurement sites. Both datasets are assumed to come out of the underlying distribution of the variable of interest. The observed measurements are assumed to have classical measurement error associated with them, whereas the areal data have an associated bias. Following these assumptions, the underlying distribution is estimated in a Bayesian context.

Dynamical Downscaling is the term used with regard to the application of a Regional Climate Model (RCM) using Global Climate Model (GCM) boundary conditions. GCMs are often measured at the 100-250 km^2 grid scale, which then require downscaling with regard to local weather conditions. The use of an RCM in this case is a mechanistic model approach allowing detailed approximation of the climate at a finer scale. Statistical Downscaling, in contrast, is defined as the process of relating climate at one scale to local climate at a finer temporal or spatial scale with regard to chosen covariates. A range of techniques are included under this umbrella term, amongst others: Perfect Prognosis.

Sahu et al. (2010) develop a method for the spatio-temporal modelling of US deposition data in a hierarchical Bayesian context. As in the aforementioned method by Fuentes and Raftery (2005), observed data and model output are combined in a single model structure. Here however, precipitation and deposition data are modelled together, given their relationship between levels of wet deposition and precipitation.

Another Bayesian hierarchical model is presented for downscaling rainfall data in the South-West of the state of Western Australia Song et al. (2014). The relationship between mean sea level pressure (MSLP) patterns and winter rainfall over the region of interest is utilised in creating the model framework, downscaling rainfall projections from a global circulation model to point locations. MSLP and precipitation are modelled as dependent upon the same latent spatio-temporal dynamical process. This process itself is based on a first-order Markov process. The model is tested using a validation dataset. The results shows improvement relative to the Global Circulation Model results in predicting present and future rainfall values across the region of interest relative to a previously published principal components regression model for the same scenario. This method benefits from the known relationship

between air pressuure and rainfall, the former of which can be measured more accurately than the latter and with less observer effort.

Berrocal et al. (2009) develop a model for the inclusion of observed measurements and grid square data. The observed data are regressed against the gridded data; the coefficients of which are allowed to vary spatially within a Gaussian spatial structure. The observed data are then seen as true point measurements of the variable of interest, whereas the gridded model output is a explanatory variable, which can explain the variability of the observed values. Given that the gridded data are available everywhere across the region of interest, but the observed data are only at the points of the measurement sites, these sites must be considered unbiased in their location, otherwise the regression of the observed values on the model output may be biased itself.

A number of the methods described here use two sources of data input: numerical model output and observed measurements from weather stations, for example. Such an approach is useful since information on a single variable, such as rainfall can be obtained from two origins: gridded model output values are defined often by a mechanistic model based, for instance, upon past meterological events whereas the observed measurements are ground-truth point values. The data used up to this point for the nitrogen deposition and rainfall covariates in the CS analysis are interpolated from their respective ground measurements. Therefore, using this gridded data in combination with point data in a similar fashion to e.g. Berrocal et al. (2009) would be inappropriate as both data sources for each covariate are effectively the ground measurements.

Perfect prognosis is selected to be applied to the CS data in this example because of the independence of the CS sites and easy application of method to available data. As mentioned previously, altitude is likely to affect precipitation and nitrogen deposition at a local level (McClatchey, 1996). Therefore, it is a justifiably scientific approach to use altitude as the predictor variable. The success of the method depends upon the strength of this relationship, but it is assumed that the relationship between rainfall and nitrogen deposition and altitude are not spurious if they exist. Localising the relationship fitted between these climate variables and altitude allows this relationship to be flexible between sites. Perfect prognosis, or localised regression allows for the easy inclusion of prediction error in the model.

5.1.3 Perfect prognosis in detail

Perfect Prognosis is the use of empirical statistical relationships between observed values of a predictand and selected variables, which can be predicted by a model at new timepoints or spatial positions. This relationship is applied to predicted values of the 'selected variables' to obtain forecast values of the predictand: in this case study either rainfall or nitrogen deposition. In this instance, the 'selected variable' is altitude, which is not forecast, but taken from the fine-scale elevation map, and so taken to be known for each plot in the response data. Using the relationship formed between altitude and rainfall, new rainfall values for each plot can be estimated.

Observed data are available for the region of interest, both for nitrogen deposition and rainfall, but these data are the basis for the gridded model output of both these covariates. Combining the datasets of observed measurements to the gridded model output does not add any new information to the downscaling method, since the data are already inherent in the gridded data. Therefore the use of the observed measurement values in the context of spatial realignment with these datasets would therefore not benefit the process.

In order to try to estimate this local error more accurately, altitude will be used to calibrate the rainfall using local regression, then the error in this regression is re-estimated and added to each newly-predicted rainfall value at the CS plot level. Interpolation or downscaling techniques are possible methods to use in order to estimate the rainfall and nitrogen deposition at the plot level. This is a local version of the linear regression method assessed by Goovaerts (2000), where the secondary information from a digital elevation model is used to interpolate rainfall data. Since the region of interest is nearly 50 times larger than the Algarve, for which the method was tested, a local regression relationship for each CS site between rainfall and altitude is desired. If the correlations between rainfall and altitude and nitrogen deposition and altitude respectively are sufficiently high, then, according to Goovaerts (2000), it is advantageous to use a regression. The extension employed here is the inclusion of prediction errors, which may affect the necessary correlation. Also similar to this concept is the downscaling method proposed by Berrocal et al. (2009), where a regression between observed measurements and gridded data is estimated. The coefficients of the the regression are allowed to spatially vary according to a correlated Gaussian process. The output is available at the point level.

As previously stated, other abiotic covariates could be considered for the regression with rainfall and nitrogen deposition for the interpolation besides or as well as altitude (Wilby and Wigley, 2000). However, data from a digital elevation model is easily accessible, accurate and not prone to measurement error. Also, a local regression model allows for the accommodation of prediction error, where the correlation between the covariate of interest and altitude is poorer. For these reasons, the local linear regression method is preferred in predicting covariates at the plot level.

The grid estimates of covariates, which have been used in the additive models in chapter 4, are for the grid square s_i, with the coordinates (a,b) as their centroid, and x_i as the corresponding covariate estimate. Each covariate estimate is defined for the square at centroid (a,b). It is assumed in the previous model that the estimate x_i is a valid estimate for the value of the covariate X in the region s_i. The assumption is made, similar to Sahu et al. (2010), that evenly spaced gridded data are assumed to be suitable surrogate data for the grid square of which each point is a centroid. If it were the case, that X_i is uniformly distributed over $s_{a,b}$, the spatial distribution of X would be disjoint where adjacent squares have differing values. Thus there is a discrepancy between the estimated measurement for the square and for the particular plots of interest in that site. This is similar to Berkson measurement error described in subsection 1.5.1. Figure 5.1 depicts a diagrammatic relationship the CS plots, which are 200m^2 and the rainfall estimates, which are 5km^2.

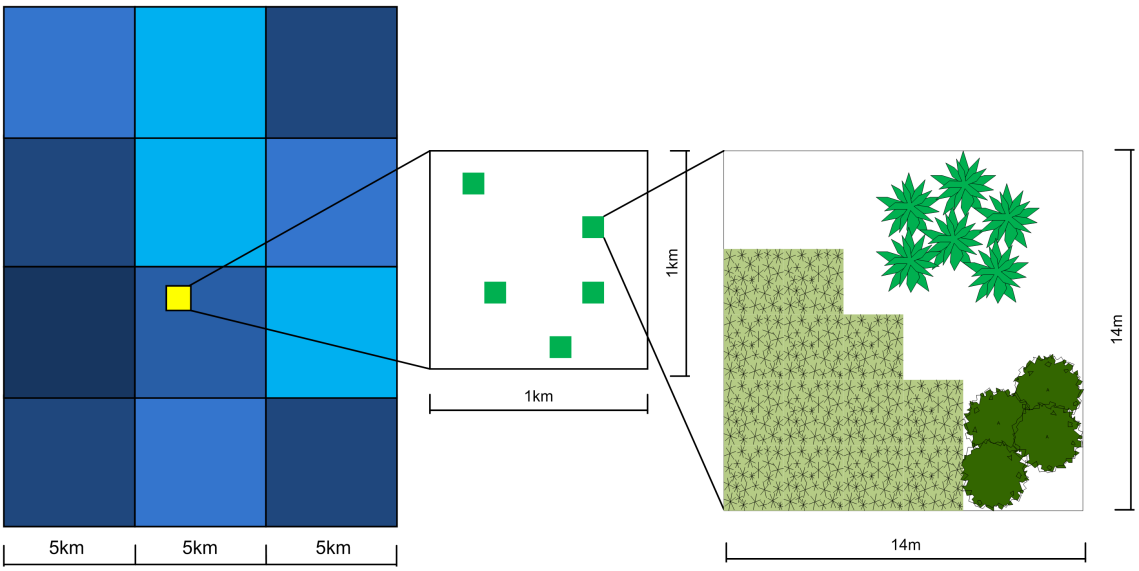

Figure 5.1: Diagram showing the relative scales of the CS plots, site and rainfall grid squares.

In discussing the Berkson error model, equation 1.6 from chapter 1 is recalled. Let a simple linear regression be considered, where Y will be fitted on X as $Y = X + \varepsilon$. However the true X is unknown and W is measured, where:

$$X = W + U_B \tag{5.2}$$

Here the error term $U_B \sim N\left(0, \sigma^2\right)$ is the Berkson error centered on zero. Berkson (1950) shows that such measurement error in an explanatory covariate as denoted in equation 5.2 does not bias the linear regression. In this simple context, taking account of Berkson error in a covariate does not change the slope of the regression, but will increase the variance of the covariate. An example of the occurrence of Berkson error in an epidemiological study is given by Armstrong (1998). When using covariates of health effects such as proximity to a source of pollution, group average exposure estimates instead of precisely measured exposure levels are subject to Berkson error. The true exposures may vary around an approximate estimate; the difference between this proxy value and the true exposure value is the Berkson error. This type of error will lead to wider confidence intervals for the slope coefficient and therefore reduce power (Armstrong, 1998).

It is predicted that the significance of the downscaled covariates in the model will decrease, leading to the inference that the estimated error added to the predicted covariate values causes extra random scatter to reduce the significance relative to the previous result. This would cause the associated standard error to increase significance of the covariate to be reduced. In a linear model scenario, pure Berkson error would result in the parameter estimate not changing, but the standard error estimate may increase and thus the covariate effect would be decrease (Schwartz et al., 2007; Zeger et al., 2000). If relationships do persist in the downscaled model, one would have more confidence in the result, given that the uncertainty has been taken into account.

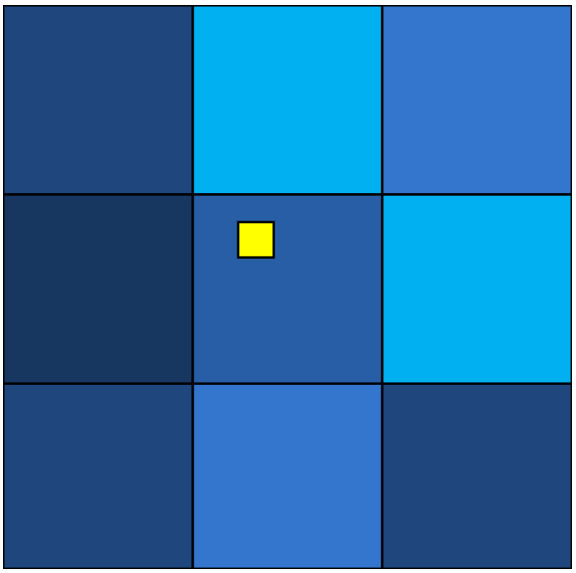

Figure 5.2: Diagram of the surrounding rainfall grid squares of the CS site, which are to be used in the downscaling process. The yellow square indicates a possible position of the CS site within the central grid square: positioned within the centre 5km^2 grid square, but misaligned with the centroid of the grid square.

Figure 5.2 shows the grid squares used in the downscaling of the rainfall estimate, for a given CS 1km^2 site. If the values of Q_i were simply interpolated from the adjacent grid square values, then the estimate of Q_i would be $E(Q_i) = N\left(r_i, \sigma^2_{R_i}\right)$, where $\sigma^2_{R_i} = Var\left(R_{ij}\right)$, and $j = 1, \ldots 9$ $(R_i = R_{i1})$. In using this method to realign the grid values, this technique would not take account of the local relationship between altitude and rainfall and nitrogen deposition. As noted by many sources, e.g. Brunsdon et al. (2001) and Smith and Fowler (2001), altitude has an effect upon both the rainfall amount and wet nitrogen deposition, which comprises the majority of total nitrogen deposition. By utilising the perfect prognosis method, the local relationships between altitude and rainfall and nitrogen deposition respectively can help downscale the covariate values. The assumption made here in this method is that the relationship between the predictand (either rainfall or nitrogen) and altitude is the same at the fine-scale as it is over the local surrounding region.

5.2 Downscaling simulation

In preliminary samples of the downscaling method there was a great deal of uncertainty associated with the downscaled values for both rainfall and nitrogen deposition. This is due

to the large amount of residual error in the perfect prognosis linear models, leading to unrealistic predictions. The downscaled data have intra-1km square variance which in are many orders of magnitude greater than the inter-square variance of the initial gridded data. Thus the covariate data available for the CS dataset are deemed unsuitable for showing the potential benefits of the downscaling methodology to providing improved results. The reason for this is the low correlation and large standard error terms associated with the local regression relationships between altitude and the respective covariates. The mean correlation between rainfall and altitude is 0.144 and between nitrogen deposition and altitude it is 0.156. In this dataset, altitude does not explain the local variability in rainfall and nitrogen deposition well, which leads to wide prediction distributions, from which the predicted values are sampled. Therefore, the downscaling method cannot improve the results with respect to the standard error of the downscaled covariates.

Given the weakness in the local regression relationships between rainfall and nitrogen with altitude respectively, the predicted values which would have been obtained from these data were too variable and thus not suitable for the downscaling procedure. This leads one to question how strong the local relationship with altitude must be, for a covariate such as rainfall to be downscaled leading to improved results in the final biodiversity regression model.

In order to test this, a simulation study will be conducted to explore the properties of the downscaling approach to estimate the relationship between biodiversity and rainfall. The simulation will attempt to recreate a situation similar to the CS data which were to be modelled, but where the model structure itself will be kept simple, with biodiversity modelled using rainfall as the sole fixed effect. A non-downscaled model will be fitted from simulated data, where the coarse rainfall at the $5km^2$ will be used as the covariate data. A downscaled model will be fitted, using the methodology outlined in figure 5.3. These models will be compared with regard to the simulated "true" relationship between biodiversity and rainfall, in order to see how the downscaling rainfall affects the resultant fitted model.

In order to test the ability of the downscaling method to improve this result, the data generated can be downscaled as in figure 5.3, where the coarse surrounding square rainfall values are regressed against coarse altitude, for each site. In order to downscale the rainfall covariate data, the perfect prognosis method will be implemented, using a simple linear regression. This will allow the altitude to help explain variability in rainfall at each site and using this

relationship, predict the rainfall at the plot level. This will also allow the remaining uncertainty to be accounted for, by sampling an additive error term from the associated prediction distribution.

The downscaled model performance will be assessed for different levels of variability between rainfall and altitude. This variability will be altered at the coarse- ($5km^2$) and at the fine-scale ($14m^2$ plot) level. The performance of the downscaled and non-downscaled models with respect to the level of variability at both scales will be analysed. The resultant change in the biodiversity model will be recorded with regard to the value of the rainfall regression coefficient and its associated standard error and significance. The coarse level is defined at the $5km^2$ level. The simulation data will be generated as follows with a step-wise description in figure 5.3: 100 CS sites will be simulated, which are each $1km^2$ in size. The site is depicted by the yellow square in figure 5.1. 5 survey plots $k \in \{1,\ldots,5\}$, each $14m^2$ in size are located in each CS site $i \in \{1,\ldots,100\}$. The plots are depicted in green, within the $1km^2$ CS site. The coarse-scale altitude A_i in feet for each $5km^2$ square in which site i will sampled from a uniform distribution: $A_i \sim U\,(1000,3000)$. These values represent a possible range of altitudes within Great Britain. Feet is used as the unit of measure here, in order that plausible rainfall values in milimetres can be sampled from the altitude data directly. The fine-scale altitude at each $14m^2$ plot k in each site i, based on the coarse-scale altitude at each $5km^2$ square i is sampled as: $A_{ik} \sim N(A_i, 100)$ The fine-scale rainfall at each plot k in site i is based on the fine altitude at that plot: $RF_{ik} \sim N\left(A_{ik}, \sigma^2_{RF}\right)$.

The biodiversity, B_{ik} at each plot is assumed to have a simple relationship with the fine-scale rainfall at each $14m^2$ plot, such that: $B_{ik} = RF_{ik} + \varepsilon_{ik}$, where the slope is assumed to have a value of 1 and ε_{ik} is a normally distributed error term. Thus the biodiversity measure can be sampled as

$$B_{ik} \sim N\left(RF_{ik}, 10\right) \tag{5.3}$$

The biodiversity response has been generated up to this point. The next stage involves generating the coarse altitude and rainfall data for the $5km^2$ squares associated with the $1km^2$ CS site. The coarse-scale altitude for the eight $5km^2$ squares j surrounding the square in which site i is located, including the square are sampled as

$$A_{ij} \sim N(A_i, 100) \tag{5.4}$$

The rainfall for each of the nine 5km^2 squares j associated with each site i, based on the altitude for that same 5km^2 square are sampled as:

$$RS_{ij} \sim N\left(A_{ij}, \sigma^2_{RS}\right) \tag{5.5}$$

where the rainfall value co-located with the site i is RS_{i1}. The biodiversity values B_{ik} can be regressed against the coarse rainfall values, RS_i in a mixed model structure where Site is included as a random effect:

$$B_{ik} = RS_i\beta + \mathbf{Zb} + \varepsilon_{ik} \tag{5.6}$$

where β is the coefficient term to be estimated, the vector $\mathbf{b} \sim N(0, \phi_\theta)$ and the error term $\varepsilon_{ik} \sim N\left(0, \sigma^2_S\right)$.

Downscaling for rainfall is conducted thus: For every 1km^2 survey site, there exists a 25km^2 square in which it is positioned and (up to) eight other terrestrial 25km^2 squares adjacent to it as displayed in figure 5.1. Thus, there is a maximum of nine 25km^2 squares associated with each survey site. The estimates of rainfall and mean altitude for each 25km^2 region are thus interpreted as belonging to a specific survey site. For each site, linear regression is then conducted for the rainfall values, using the mean altitude of each surrounding 25km^2 region as an explanatory variable. A realigned value of rainfall is required for each plot k at each site i. Thus, for every site i, the regression equation is formed as follows:

$$RS_{ij} = \alpha_i + A_{ij}\beta_i + \varepsilon_{ij} \tag{5.7}$$

where RS_{ij} is the estimated rainfall and A_{ij} is the mean altitude associated with the 5km^2 grid square j around site i, α_i and β_i are model parameters and $\varepsilon_{ij} \sim N\left(0, \sigma^2_\varepsilon\right)$. So, in order to obtain new predictions for rainfall estimates at the 200m^2 plots, a finer-scale altitude map is used; in this case, it is calculated using altitude radar measurements at the plot level. The finer-scale altitude values, termed a_{ik}, are used to predict the rainfall at a new location k in site i, where $E(Q_{ik})$ is the expected rainfall, calculated by the equation:

$$E(Q_{ik}) = r(a^*_{ik}) = \alpha_i + \beta_i a^*_{ik}$$

In the above equation, a^*_{ik} is the plot altitude at plot k in site i. However, the calculated rainfall is only a point estimate; the error term in the regression is not taken account of here. Instead q_{ik} is calculated by the following equation:

$$Q_{ik} = r^*_{ik} + SE\left[r\left(a^*_{ik}\right)\right]\eta \tag{5.8}$$

where $\eta = t_\nu$, randomly sampled from the t-distribution with $\nu = 7$ degrees of freedom, since there are 9 rainfall values used in the regression in equation 5.7.

New predicted rainfall values are sampled at the fine-scale plot level, using the altitude at each plot. The biodiversity measures can now be regressed against the downscaled rainfall values:

$$B_{ik} = \beta Q_{ik} + \mathbf{Zb} + \varepsilon_{ik} \tag{5.9}$$

where Site is again included as a random effect and with the same error structure. The split covariate downscaled model is structured as:

$$B_{ik} = \beta_1 RS_{i1} + \beta_2\left(Q_{ik} - RS_{i1}\right) + \mathbf{Zb} + \varepsilon_{ik} \tag{5.10}$$

1. $1km^2$ CS sites i ϵ [1,100] defined which are each positioned within unique 5km grid squares i.

2. Sample the coarse altitude A_i (in feet) at each $5km^2$ grid square i identified in 1., using a uniform distribution:

$A_i \sim U(1000,3000)$

3. Sample the fine-scale $14m^2$ plot-level altitude A_{ik} for each CS plot k ϵ [1,5] in site i from a Normal distribution with mean A_i and variance 100:

$A_{ik} \sim N(A_i, 100)$

4. Sample the the fine-scale $14m^2$ plot-level annual rainfall R_{ik} at each plot k at site i from a Normal distribution with mean A_{ik} and variance σ_{RF}^2:

$R_{ik} \sim N(A_{ik}, \sigma_{RF}^2)$

5. Sample the biodiversity in each plot k from a Normal distribution with mean R_{ik} and variance 10:

$B_{ik} \sim N(RF_{ik}, 10)$

6. Sample the surrounding altitude values A_{ij} for the grid squares j ϵ [2,9] adjacent to each $5km^2$ site i from a Normal distribution with mean A_i and variance 100:

$A_{ij} \sim N(A_i, 100)$

7. Sample the rainfall for the $5km^2$ grid squares j ϵ [1,9] from a Normal distribution with mean A_{ij} and variance σ_{RS}^2 ($A_{i1} = A_i$, the central $5km^2$ grid square):

$RS_{ij} \sim N(A_{ij}, \sigma_{RS}^2)$

8. Fit the non-downscaled model of biodiversity against coarse 5km grid square rainfall:

$B_{ik} = \alpha + RS_{i1}\beta + \mathbf{Zb} + \varepsilon_{ik}$

9. For each site i, regress the nine 5km square rainfall values against the corresponding altitude values:

$R_{ij} = \alpha_i + A_{ij}\beta_i + \varepsilon_{ij}$

10. Predict the rainfall at each plot k in site i, using the equation in 9:

$q_{ik} = \alpha + z_{ik}\beta_i + SE[r(a_{ik}^*)]\eta$, where $\eta = t_\nu$, randomly sampled from the t-distribution with $\nu = 7$ degrees of freedom.

11. Fit the downscaled model of biodiversity against predicted plot rainfall values:

$B_{ik} = \alpha_i + Q_{ik}\beta_i + \mathbf{Zb} + \varepsilon_{ik}$

12. Fit the downscaled split covariate model of biodiversity against predicted plot rainfall values:

$B_{ik} = \alpha_i + \beta_1 R_i + \beta_2(Q_{ik} - R_i) + \mathbf{Zb} + \varepsilon_{ik}$

13. Repeat steps 10-12 for 10 simulations and calculate the median of the rainfall coefficient and associated standard error.

13. Repeat steps 1-12 for 1000 simulations and record the estimated rainfall coefficient and associated standard error for each model in steps 8 and 11-13 and simulation run.

14. Repeat steps 1-13 for different values of σ_{RF}^2 and σ_{RS}^2 and collate the results.

Figure 5.3: Description of the simulation process in order to test the downscaling methodology.

In order to more accurately estimate any change in the resultant model, this simulation is run 1000 times for each unique choice of σ^2_{RF} and σ^2_{RS}. The mean estimated coefficients, β for both the non-downscaled and downscaled models as well as the standard error associated with the coefficient term will also be recorded and compared against the "true" β value of 1. The simulation was set up as follows: values for the fine-scale and coarse-scale variances σ^2_{RF} and σ^2_{RS} are chosen. With these values defined, figure 5.3 details the simulation process.

5.2.1 Simulation results

The results are shown in figure 5.4, where the coefficient of rainfall in the downscaled model is centred around 1, in comparison with the non-downscaled, which has a wider range of estimated coefficient values. The scales for the graphs at figure 5.4 are identical, given the difference in values returned by the different models. The standard error terms for the rainfall coefficient in the downscaled model are all much smaller in comparison to the non-downscaled model.

The performance of the downscaled and non-downscaled model coefficients in the simulation are shown in figure 5.4, 5.5, 5.6 and 5.7. For the non-downscaled model, the mean standard error of the estimated value increases as the intra 5km grid fine-scale variance (σ_{RF}) increases. The coarse-scale (between 5km grid) variance has no impact upon the model result, as the true rainfall and 5km gridded rainfall values are unaffected by change in this variable. The downscaled model performance is more sensitive to changes in the coarse-scale variance σ_{RS} as this increases the uncertainty associated with the downscaled predictions, leading to a broader prediction distribution from which the samples are drawn (Figure 5.6).

Over the range of values tested, the 90% interval for the downscaled model coefficient is smaller than for the non-downscaled model, indicating greater precision in the estimates obtained (Figure 5.5). The downscaled model intervals do show accelerated widening as the coarse and fine-scale variance levels are increased, from 0.003 to 0.018, relative to the non-downscaled model, which has a minimum of 0.025 and maximum of 0.031. The change in the size of the two variance parameters appear not to have an interactive effect upon the size of the non-downscaled model interval.

Over the range of values tested, the mean estimated standard error and the 90% interval of the standard errors are smaller for the downscaled model than for the non-downscaled model. The size of the mean standard error for the non-downscaled model differs only very slightly

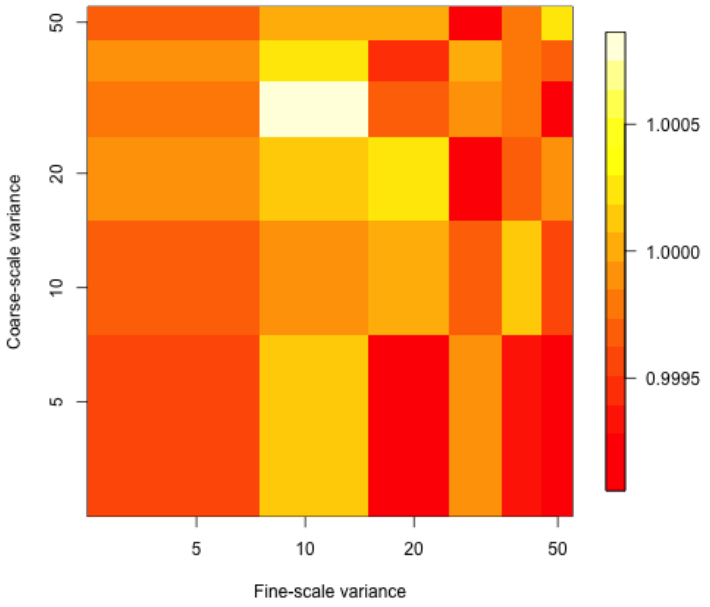

Figure (a)

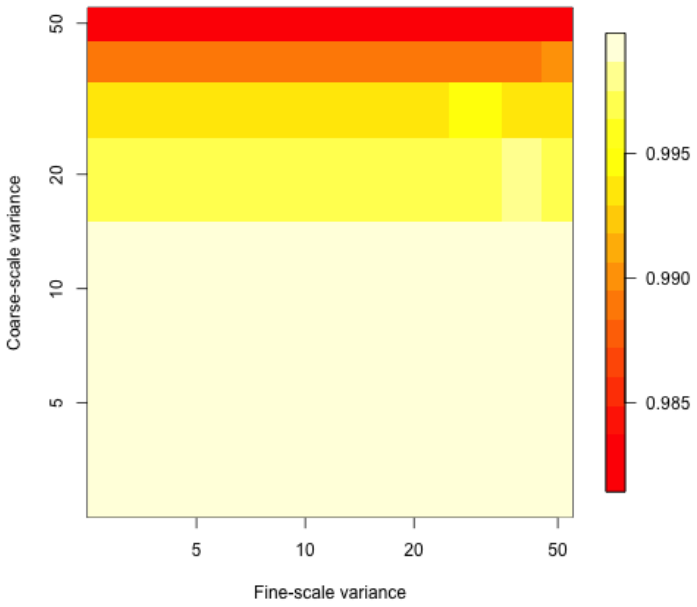

Figure (b)

Figure 5.4: The two graphs show results of the downscaling simulation. The median estimated rainfall coefficient for each tested pair of variance values is displayed by a heat map: figure (a) is the non-downscaled model; figure (b) the downscaled model.

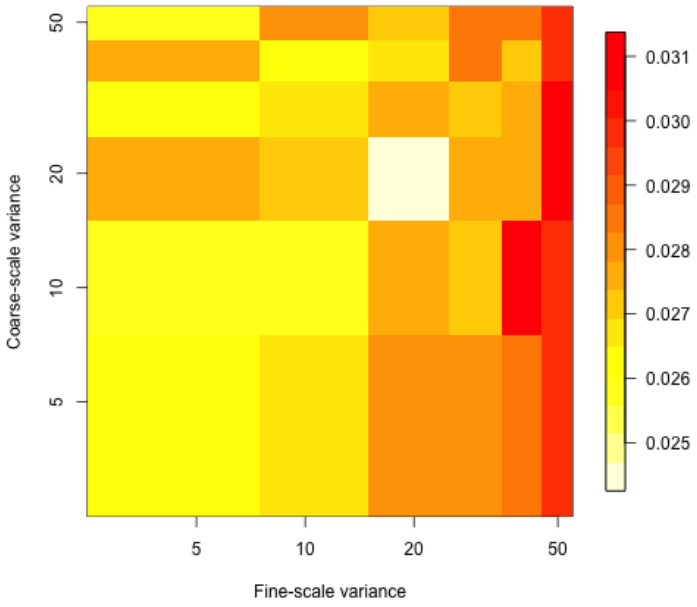

Figure (a)

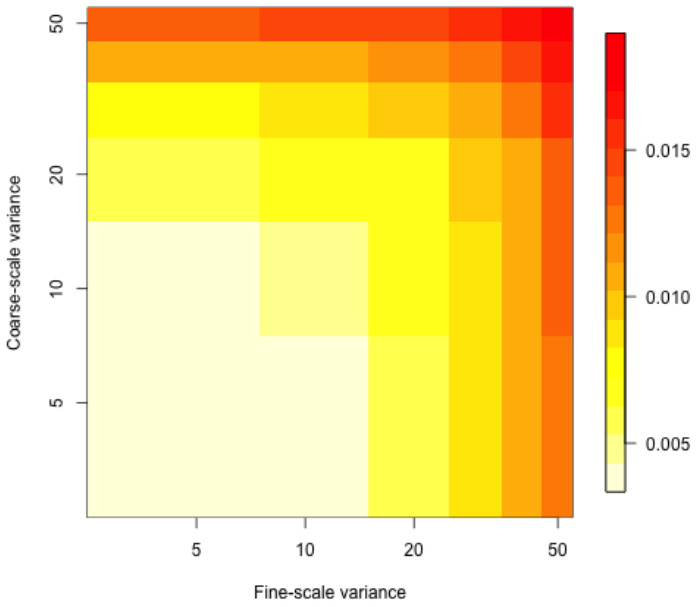

Figure (b)

Figure 5.5: The two graphs show results of the downscaling simulation. The centre 90% range of the estimated rainfall coefficient for each tested pair of variance values is displayed by a heat map: figure (a) is the non-downscaled model; figure (b) the downscaled model.

over the range of variance values tested from 0.008 to 0.009, whereas the downscaled model shows a much larger shift, from 0.001 to 0.007.

The performance of both models appear comparable for low values of σ_{RF} and σ_{RS}. Figure 5.8 shows 50 random samples of the individual simulation results when σ_{RS} and σ_{RS} are both equal to 20. The downscaled model parameter estimates are much closer to the true slope of 1 than the non-downscaled coefficients, but the downscaled model fits also appear to be slightly negatively biased. The standard errors of the downscaled coefficients are much smaller than for the non-downscaled model. A more precise coefficient estimation in the downscaled model is therefore disadvantaged by the incursion of bias into the coefficient estimate.

The deterioration in the performance of the model as the variance values are increased is exemplified in figure 5.9, as the downscaled model coefficient estimates are much smaller than in figure 5.8. The non-downscaled model results, when the coarse-scale variance is set to 50, appear similar to those when the variance is set at 20. The bias in the downscaled model estimates is much noticeable as a result of the increase in this coarse-scale variance; all downscaled coefficient estimates in figure 5.9 have values below 1.

It is against this criterion that the usefulness of the downscaling process developed should be tested: does the eventual downscaled model have better performance in terms of covariate prediction and precision than the non-downscaled model? Figure 5.8 shows that the downscaled model can deliver improved results clearly, where a sample of the model results are shown. The downscaled model results show coefficient estimates with a smaller distribution than the non-downscaled model about the the true regression line and smaller standard errors. There is a slight negative bias in the downscaled results. This indicates an increase in the precision of the downscaled model at these variance values, but a decrease in the accuracy of those results.

5.2.2 Split downscaled covariate simulation

In order to look more closely at the effect of downscaling the rainfall covariate, the same simulated data were used to regress the biodiversity response against the coarse 5km gridded rainfall data and a separate covariate of the difference between the 5km gridded values and

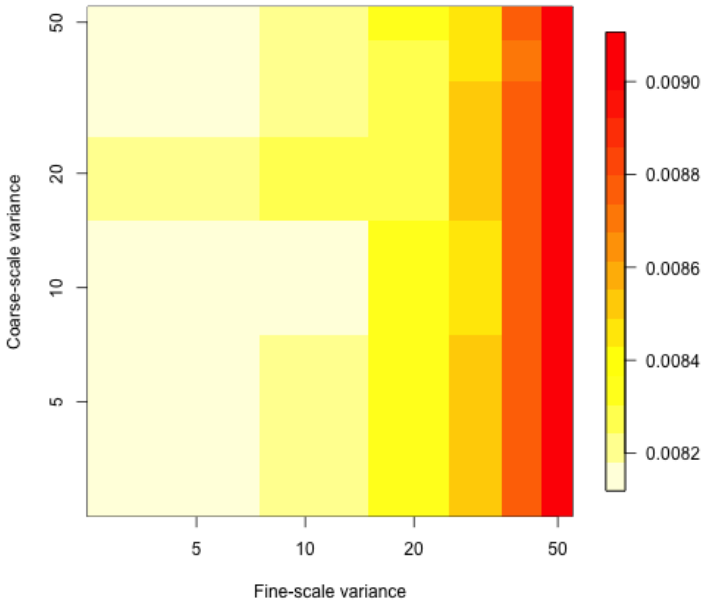

Figure (a)

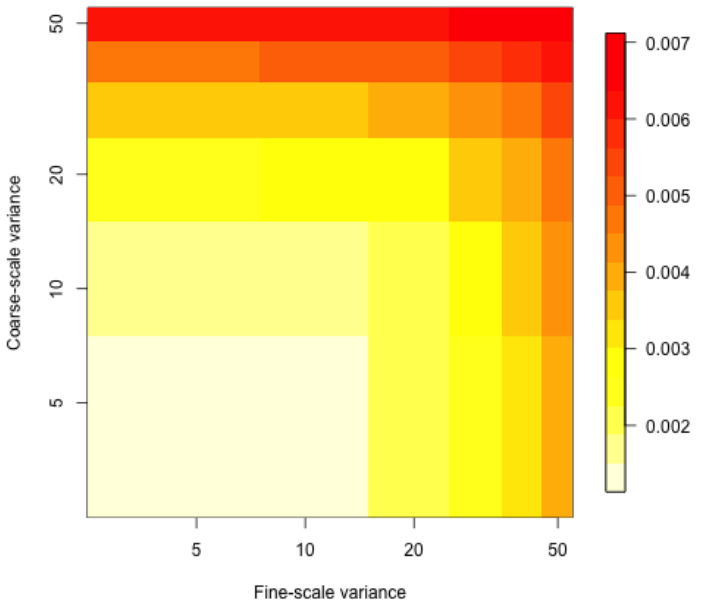

Figure (b)

Figure 5.6: The two graphs show output from the downscaling simulation; the mean estimated standard error for the rainfall coefficient for each tested pair of variance values is displayed by a heat map: figure (a) is the non-downscaled model; figure (b) is the downscaled model.

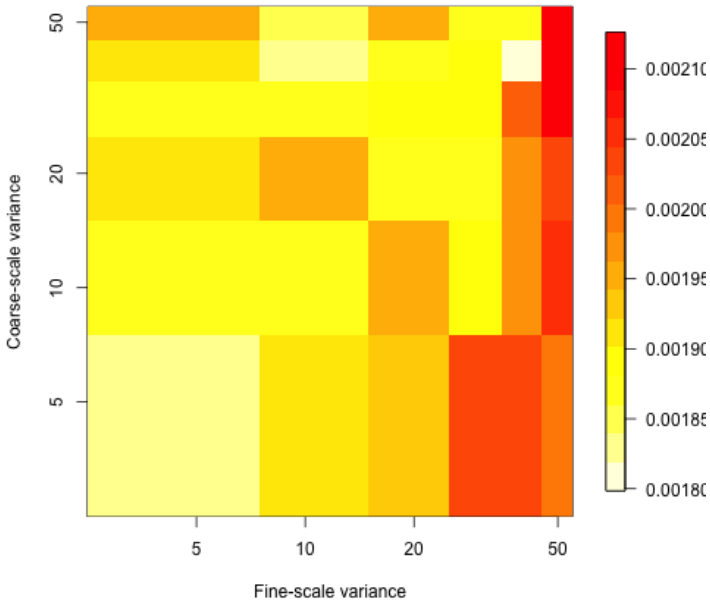

Figure (a)

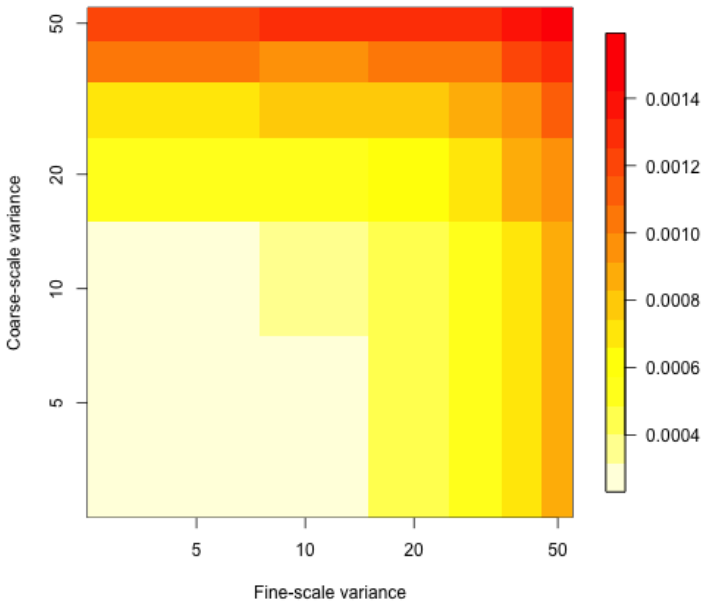

Figure (b)

Figure 5.7: The two graphs show results of the downscaling simulation. The centre 90% range of the estimated standard errors for the rainfall coefficient for each tested pair of variance values is displayed by a heat map: figure (a) is the non-downscaled model; figure (b) is the downscaled model.

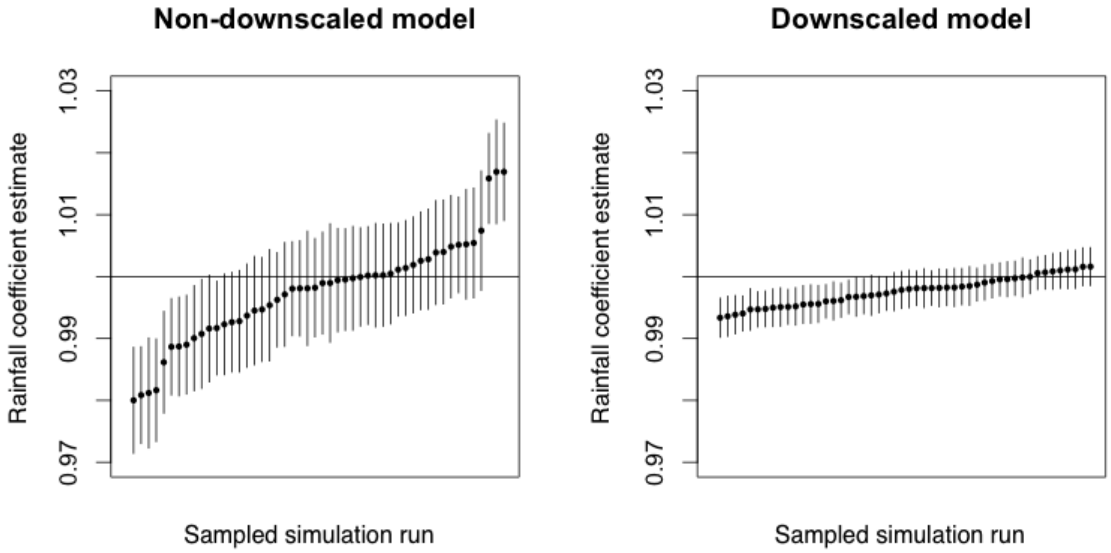

Figure 5.8: Of the 1000 simulation runs for a particular pair of variance values (σ_{RF} and σ_{RS} both equal to 20) 50 have been randomly sampled and in fitting the biodiversity response, the rainfall coefficient estimate and standard error bars for each unique sampled simulation run are displayed. The true slope of 1 is shown for reference. The results have been ordered to show the range more clearly.

the downscaled covariate term. In so doing, the downscaled covariate is split into these two components.

The heat maps shown in figures 5.10 and 5.11 display the results in the same manner as for the separate downscaled and non-downscaled rainfall models. The value of the mean coefficient term for the non-downscaled component of rainfall are similar to those for the non-downscaled model in figures 5.4 and 5.6.

The advantage of splitting the downscaled covariate into its constituent parts of non-downscaled rainfall and the downscaled difference would allow one to see how the downscaled covariate improves the coefficient estimation in the model. From the downscaled model with a single covariate, the coefficient had a slight negative bias, which was exemplified in figures 5.8 and 5.9. The non-downscaled model coefficient, at all tested variance values, has a distribution centered on the true value of the coefficient: 1.

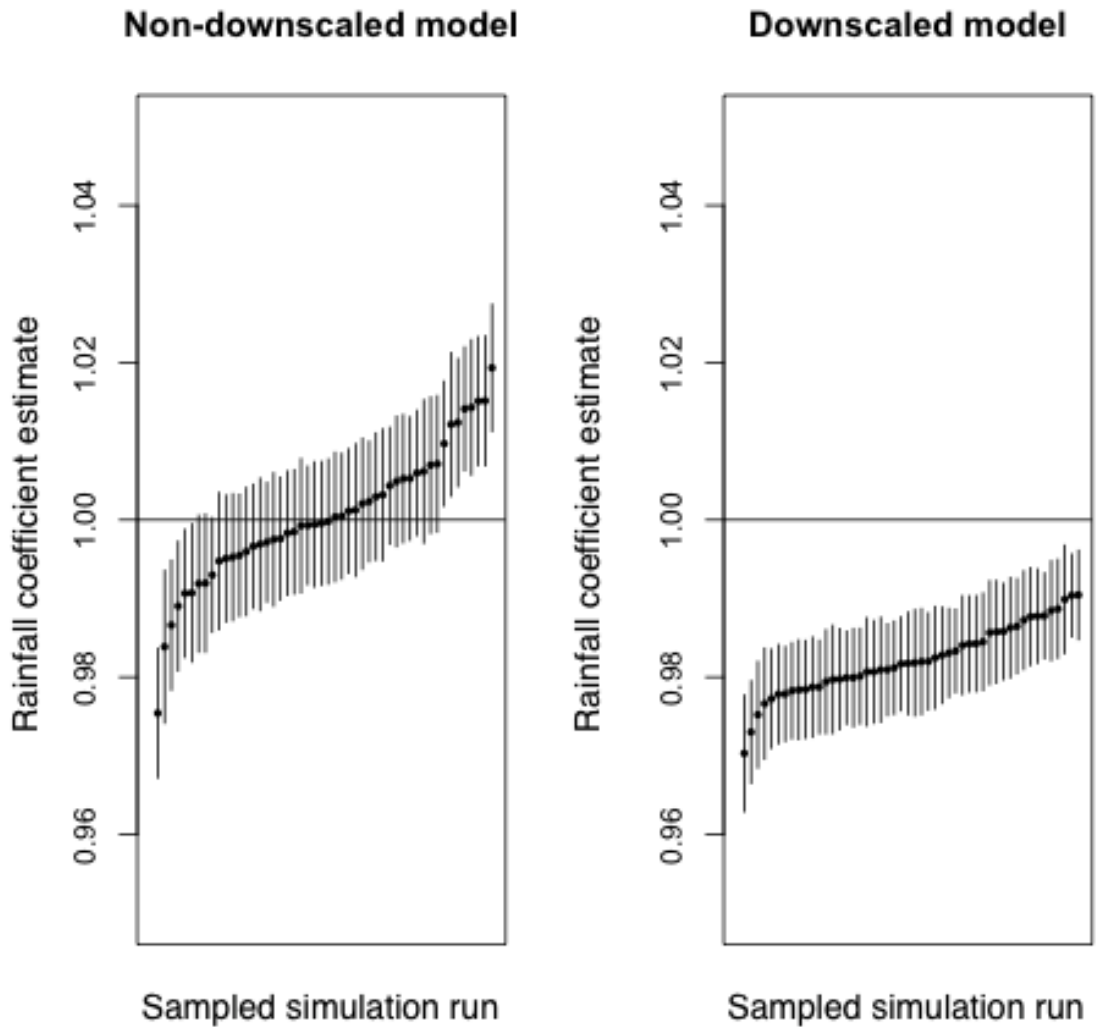

Figure 5.9: Of the 1000 simulation runs for a particular pair of variance values (σ_{RF} and σ_{RS} equal to 20 and 50 respectively) 50 have been randomly sampled and in fitting the biodiversity response, the rainfall coefficient estimate and standard error bars for each unique sampled simulation run are displayed. The true slope of 1 is shown for reference. The results have been ordered to show the range more clearly.

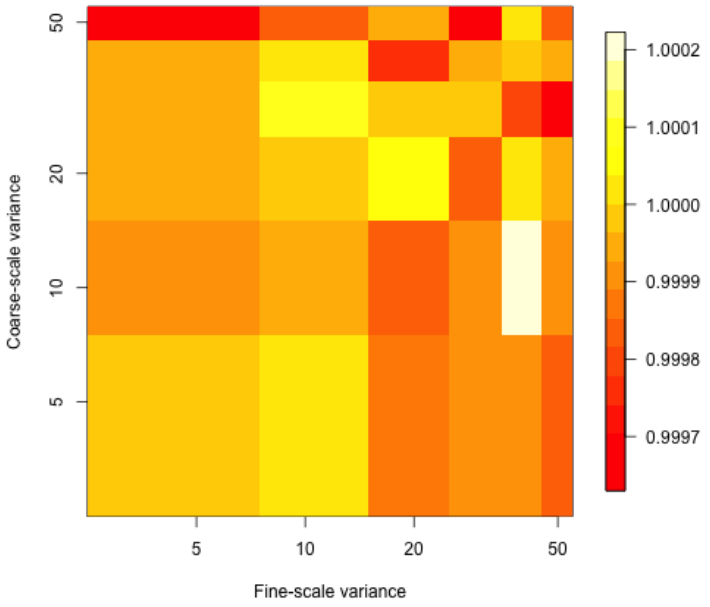

Figure (a)

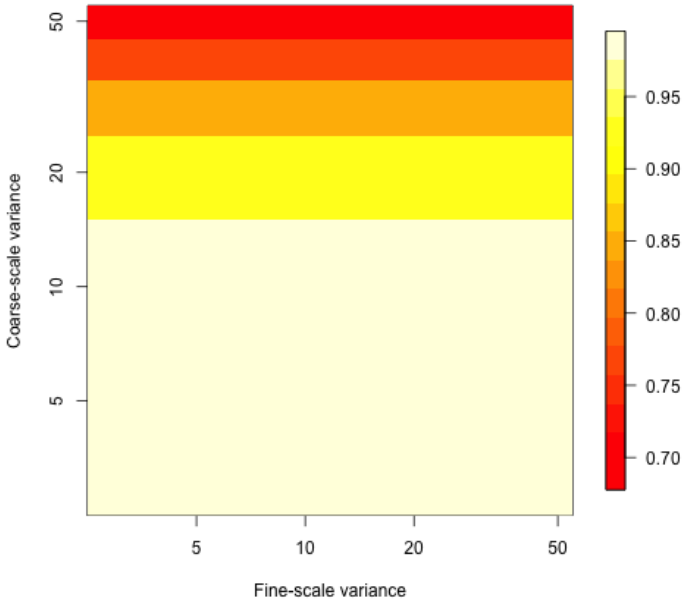

Figure (b)

Figure 5.10: Mean coefficient of rainfall for the downscaled split covariate simulated model containing the coarse 5km^2 rainfall term (figure (a)) and the downscaled difference rainfall term (figure (b)). The results are similar as for the singular simulation data models, but with much poorer performance of the downscaled component.

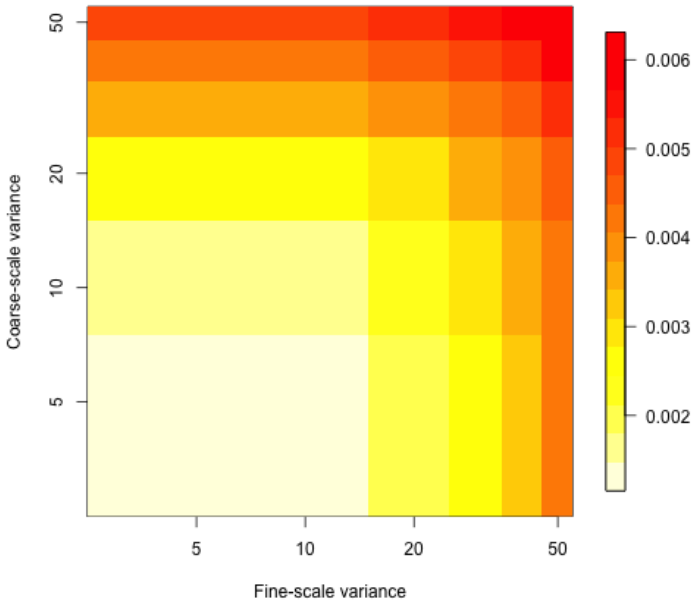

Figure (a)

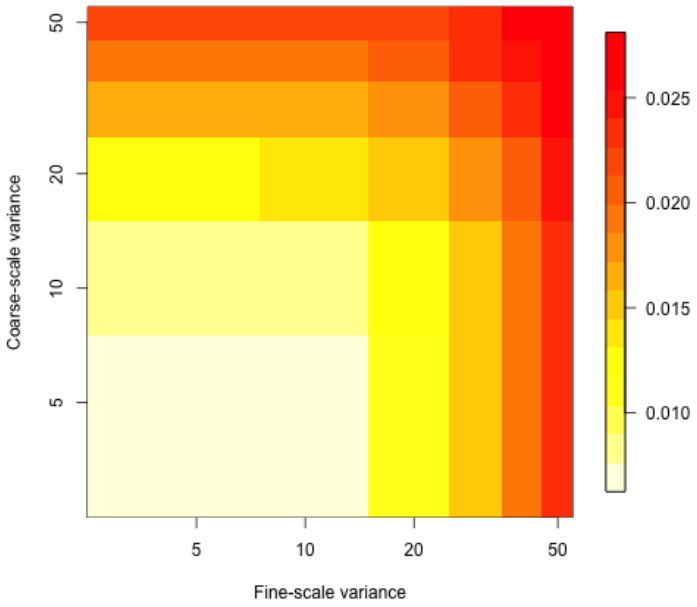

Figure (b)

Figure 5.11: Mean standard error of the estimated rainfall coefficient for the downscaled simulated model containing the split rainfall covariate; figure (a) refers to the non-downscaled covariate coefficient; figure (b) depicts the coefficient corresponding to the difference between the non-downscaled and downscaled covariates. The results are similar as for the singular simulation data models, but with clearly poorer performance of the downscaled component.

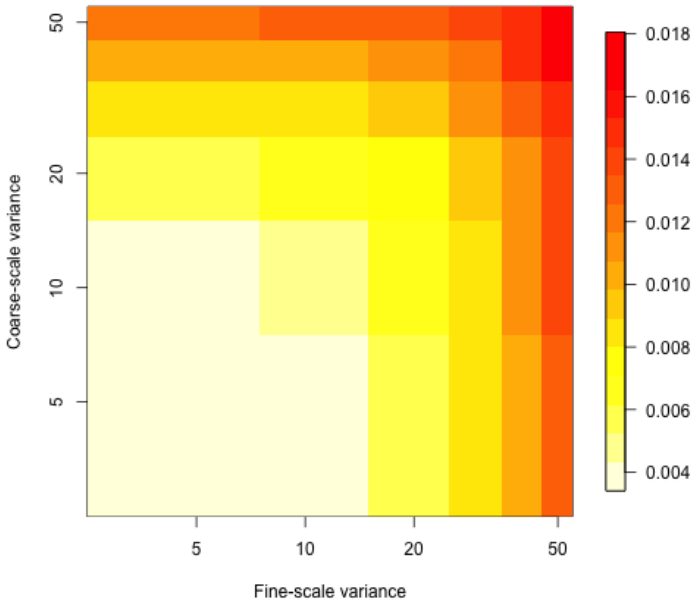

Figure (a)

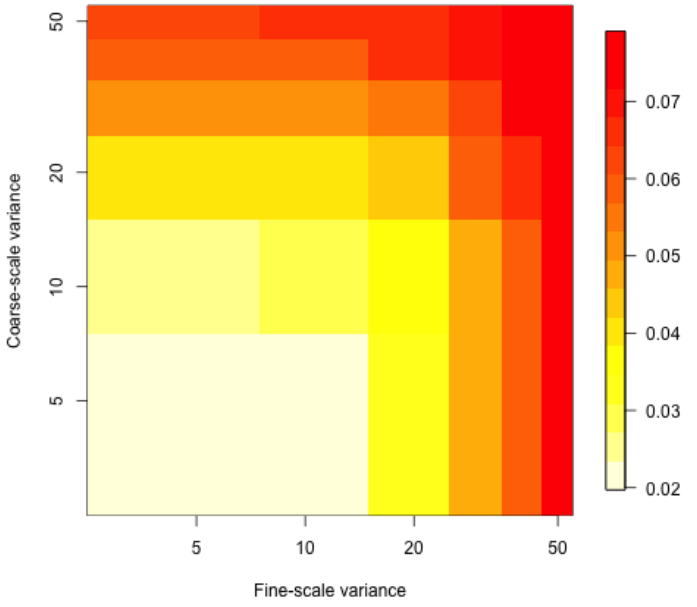

Figure (b)

Figure 5.12: The two graphs show results of the downscaling simulation. The central 90% range of the estimated rainfall coefficients for each tested pair of variance values is displayed by a heat map: figure (a) is the non-downscaled covariate coefficient; figure (b) is the coefficient corresponding to the difference between the non-downscaled and downscaled covariates.

In splitting the rainfall covariate into the non-downscaled and downscaled components, one can see the downscaled mean difference covariate has a negative bias as in the single model, whereas the mean non-downscaled component coefficient has very little deviation from the true coefficient value. The estimated mean value of the coefficient for both covariates is shown in figure 5.10. The non-downscaled covariate has a smaller 90% interval than the downscaled covariate. The mean standard error associated with the downscaled covariate is much larger than for the non-downscaled covariate in figure 5.11. This indicates that in downscaling the rainfall covariate with the aid of altitude values, the estimated standard error is greater than the difference between the gridded covariate value and the new realigned value, thereby reducing the significance of the covariate itself.

The standard error of the non-downscaled covariate is affected by the inclusion of the downscaled covariate; the mean standard error in figure 5.11 is shown to increase for both covariates as the coarse-scale variance increases; a pattern which patently does not occur in the non-downscaled model in figure 5.4.

In order to investigate how the correlation between rainfall and altitude is related to the tested variance values, the correlation of the simulated data was calculated. Figure 5.13 displays the mean correlation between rainfall and altitude calculated for each variance level in the simulation. As could be expected, lower correlation is obtained when the variance, either fine- or coarse-scale, is greater.

The performance of the downscaled rainfall values in figure 5.4 at coarse-scale variance values of 20 or greater is poor relative to the non-downscaled model. From figure 5.13, it can be seen that the correlation of rainfall and altitude is still above 0.9 with this level of variance simulated. From this it can be inferred that the correlation between the variable to be downscaled and the covariates used in this downscaling step should be very high at the coarse-scale in order that the downscaling method is successful.

This simulation was conducted with the possibility of using the method for the downscaling of the rainfall and nitrogen deposition data in the regression model in chapter 4. The mean correlation of the 1998 rainfall values and altitude for the region of nine grid squares surrounding each CS site is approximately 0.35. For the nitrogen deposition data, the mean

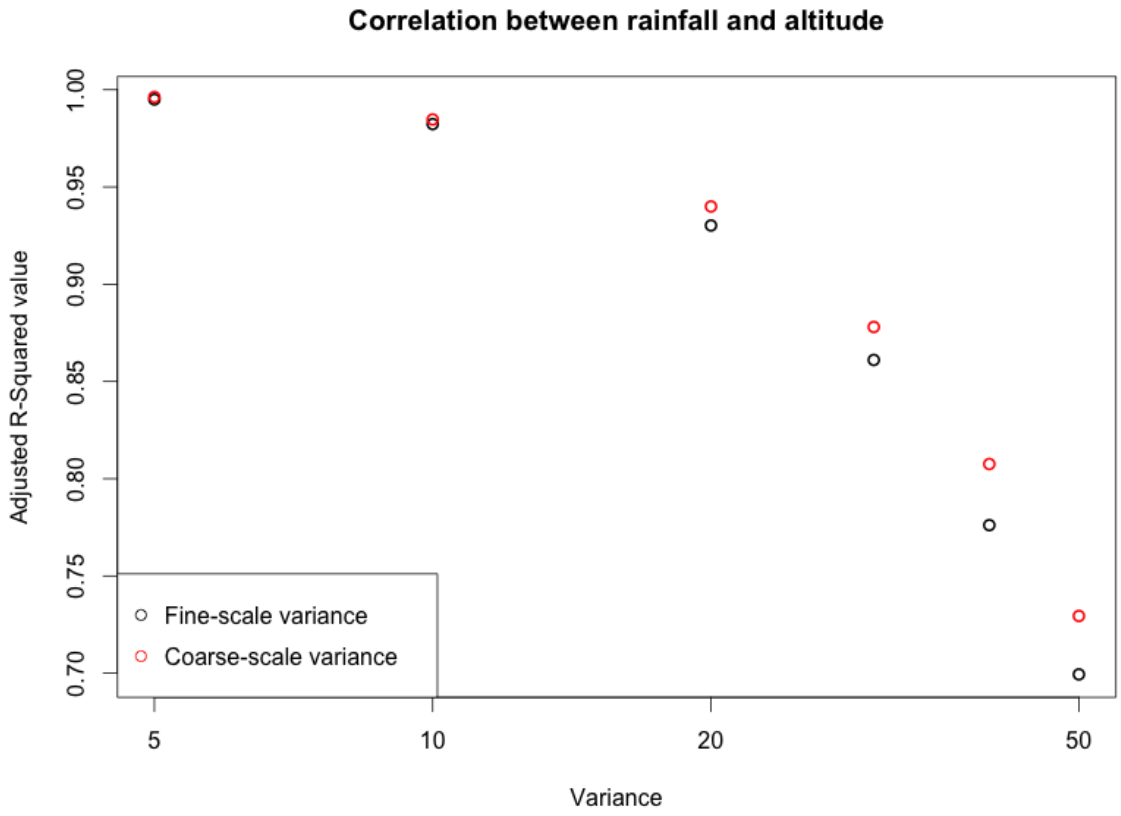

Figure 5.13: The mean correlation between the rainfall and altitude values is plotted against the simulated variance values at the fine- and coarse-scale for the 1000 simulations. A clear negative correlation is shown between the correlation coefficient and the size of the variance in the simulation. The coarse-scale correlation is slightly higher than the fine-scale variance, due to there being nine data values at that scale, as opposed to only five at the fine-scale.

correlation with altitude is about 0.2. On the basis of these relatively low values, it is decided that the downscaling method is inappropriate for the data avaiable.

5.2.3 Simulation evaluation

The performance of the non-downscaled model is affected by the fine-scale variance only, as the coarse-scale variance has no effect on the rainfall values within the central 5km^2. The coefficient estimates show only a slight increase in bias as the fine-scale variance increases. Over the range of variance values tested, the bias is very slight. The mean of the coefficient standard error increases as the fine-scale variance increases, since the correlation between biodiversity and the rainfall values is then lower, due to greater variation around the regression line.

The downscaled model performance is affected primarily by the coarse-scale variance, as can be seen in the coefficient estimate mean. The magnitude by which the downscaled model coefficient mean is affected by the coarse-scale variance is of two orders greater than that which the non-downscaled model coefficient mean is affected by the fine-scale variance. The fine-scale variance affects the downscaled model, but the size of the effect is much smaller, compared to the influence of the coarse scale variance.

As could be expected, the lower the coarse-scale variance, the better the downscaled model performance, in terms of the mean coefficient estimate. The lower the variance at the fine-scale, the better the downscaled model performs, although this is not as influential on the result obtained as the coarse-scale variance. The standard error, however is affected by increases in both coarse-scale and fine-scale variance, although more by an increase in coarse-scale variance.

The downscaled model outperforms the non-downscaled model when the variability between rainfall and altitude is very low, ensuring a narrow prediction distribution and thus more precise estimation of the regression between biodiversity and rainfall. The coarse-scale variance influences the downscaled model performance more than the fine-scale variance and also more than the non-downscaled model is affected by fine-scale variance. The non-downscaled model, *a priori*, is unaffected by coarse-scale variance.

Where both the fine- and coarse-scale variances are small, i.e. 10 or less, the downscaled and non-downscaled models are comparable and the downscaled model outperforms the non-downscaled model when the coarse-scale variance value is 5. The loss of model performance when the coarse-scale variance is 20 and the adjusted r-squared value is greater than 0.9 indicate very clearly that the correlation between the downscaled variable and its predictor covariate at the coarse-scale is pertinent to the success of the downscaling method.

Classical measurement error appears to be incurred in the downscaling process, given the slight negative bias of the mean estimated coefficient, as the coarse-scale variability increases. This was due to the large width of the prediction distribution at larger coarse-scale variance values. The non-downscaled model, mean coefficient on the other hand, shows very little sign of bias, despite the increase in fine-scale variance.

For the downscaled model with a split rainfall covariate, the mean estimated coefficient of the non-downscaled component shows little bias, but the standard error increases as the coarse-scale variance is increased. The simulation structure assumed a common relationship between rainfall and altitude at both the coarse- and fine-scale; it was only due to changes in the variance of this relationship at the two respective scales that changes in the result were assessed. The effect of different 'true' regression lines between rainfall and altitude at the two scale was not investigated.

In some of the heat maps, particularly those for the non-downscaled models, the image does not show an even spatial pattern, indicating a smooth gradient of simulation results. This indicates that the results have converged to a defined value over 1000 runs of the simulation. In all instances, the differences between the non-downscaled and downscaled models are very obvious with the results alreadys obtained, rendering the convergence of the non-downscaled superfluous to the conclusions drawn in this analysis. This convergence would be important if one wished to define the exact point at which one should use the downscaling method in order to obtain optimal results in the biodiversity model. Only six variances values were tested, meaning 36 possible combination of variances for the coarse- and fine-scale respectively. Interpolation of the variances or a greater number of variance values tested could help improve the understanding of this trend.

5.3 Discussion

The aim of this chapter was to create a framework for donwscaling spatially misaligned covariate data to the response locations. The example data set used in this chapter was take from the Countryside Survey, first outlined in chapter 4.

The downscaling method was motivated by a need both to realign the environmental covariate data to the location of the plots and also to estimate the uncertainty associated with the realignment. The uncertainty in rainfall and nitrogen deposition estimates would be estimated by using a local regression with altitude to form local prediction distributions for these covariates, in a method similar to Perfect Prognosis downscaling. Perfect prognosis was chosen as the method for conducting the realignment, given the ability to use altitude as a predictor in a local regression for each CS site. Random samples could then be drawn from this prediction distribution to re-estimate the rainfall and nitrogen deposition at a finer scale for each individual plot site.

The high variability in the predicted rainfall and nitrogen deposition values as well as the low mean correlation between the respective covariates and altitude at the $5km^2$ grid coarse-scale led to the need for a simulated dataset in order to show the viability of the downscaling methodology in improving the resultant model of biodiversity. The simulation used 100 sites, at which altitude and rainfall data at the coarse- and fine-scale is simulated. The simulated biodiversity indices for each plot have a strong correlation with the "true" fine-scale rainfall. The $5km^2$ grid rainfall values are used as the sole fixed effect covariate in the non-downscaled model. This model was compared against the downscaled model, where the downscaled rainfall values using the surrounding relationship between rainfall and altitude were used as the sole fixed effect, in order to see how well both models estimated the relationship between biodiversity and rainfall. Repeated simulation allowed mean estimates of the rainfall coefficient and associated standard error to be calculated from the compiled results.

The downscaled method was shown to be a slight improvement in model performance of biodiversity when the fine- and coarse-scale variance between predictor and predictand are both very small. Increase in the coarse-scale variance results in a biased estimate of the rainfall coefficient with an slight attenutation towards zero. This is deemed to be the effect of the prediction distribution creating much more variable covariate values and in turn, a shallower regression line.

Given that some of the actual data values used in the GAM structures in chapter 4 were considered to have too much variability attached to them, it may be that other effects such as the aspect or gradient of the land, or meteorological effects which can affect the rainfall and nitrogen deposition as well, need to be considered when downscaling such data. A multiple linear regression downscaling model could be applied in this case, if fine-scale spatial and temporal data were available. The rainfall data was only available at the 5 km grid square level; more precise predictions of the rainfall may have been achieved, were 1km annual rainfall maps of Great Britain able to be utilised. Other model types, such as GAMs were not explored for the 'Perfect Prognosis' downscaling step. The altitude values that are used in the prediction stage of the downscaling method are at the 100m grid level, so also have a degree of variability within them. This is not estimated within the model; a finer-scale elevation map was not used, since the locations of the CS sampling plots is only known at the 100m level.

There is no known uncertainty associated with the rainfall gridded values. However, if there were, this would also need to be taken into account in the downscaling process, and as a result a still larger error associated with the covariate coefficient would be returned. If the uncertainty were known, another downscaling method may be more suitable, to utilise this extra information rather than adding to the variation in the present model.

With this in mind and looking beyond this analysis, there are many future modelling challenges in this field of study. Consideration of the suitability of using realignment techniques at the fine-scale level, such as those developed in this case study should be considered. An evaluation of all realignment methods was not possible in these chapter. Other downscaling methods were not tested, due to lack of appropriate ground observations, such as the developed method by Fuentes and Raftery (2005), or kriging, due to the estimation of the rainfall maps. If downscaling were not a suitable option, the uncertainty in the creation of the grid square estimates themselves would help in estimating the within-square variability, using a Berkson error model. This would also prevent the negative bias of the regression estimate as observed in the simulation data in figure 5.9. However, if one ignores the possibility of within-square variability this could lead to false inferences made on the importance of covariate effects on the response.

A spatial correlation of the regression between rainfall and altitude at each CS site could be estimated, allowing for a 2-dimensional spline to be fitted over the region of interest. This

would result in a smooth interpolation of the perfect prognosis regression coefficient. This would then allow for the estimation of rainfall at locations where no rainfall values were available, but where altitude was known.

Ground-truthed measurements of rainfall and nitrogen deposition would allow the use of more complex downscaling methods, such as the approach developed by Sahu et al. (2010), involving model grid estimates of covariates and observed data from measurement sites. Rainfall and nitrogen data from the years directly preceding the survey would allow the possible lag effect of these covariates to be studied more closely.

In a similar way to the Transect-Month aggregation used in the carabid analysis, a possible technique for further development is the aggregation of the plot data in each $1km^2$. The species coverage in each plot would need to be collated, but given the assumed independence of the biodiversity in each plot, combining the plots records to obtain a univariate response may be difficult. Combining plot habitats if aggregating to the 1km grid level is not an intuitive process either.

This downscaling method could be applied to predict data at a future point in time, rather than necessarily at a different spatial scale. Such a method as perfect prognosis is suited to weather forecasting, where the covariate to be downscaled is not suitable to be used in its current form via a simple realignment method such as the Thiessen polygon. The relationship between air pressure and rainfall, for instance could be estimated as utilised in Song et al. (2014), but the use of the present rainfall values in place of those a month from now would be unsuitable. Perfect prognosis and the incorporation of prediction error as developed here lend themselves to such a situation very suitably.

In summary, the use of a realignment method for the downscaling of environmental covariate data has been developed and its capacity for usage given certain criteria has been assessed in a spatial context. Namely, the availability of a predictor covariate, in this case, altitude, is necessary, which is available at both the scale of the variable to be downscaled and the scale of the variable to be modelled. This predictor covariate must have a common relationship with the downscaled variable at both scales, otherwise the predictions of the downscaled variable would not be justified.

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Chapter 6

Conclusion

6.1 Summary

Before summarising the analysis conducted, the original questions set out in the aims of the thesis are recalled:

- What evidence is there about how biodiversity in specific communities is impacted by certain environmental drivers and pressures?
- To what extent are these specific communities driven by environmental change?
- How is fine-scale misalignment between the model covariates and the response in the environments best dealt with?
- How can the uncertainty in fine-scale model covariates be estimated?

In discussing these questions, three case studies were conducted of data from different sources in Great Britain and which were recorded at different scales. A variety of statistical regression models were used in the analysis, in order to link the model covariates and the response data in each case study. This thesis has demonstrated the implementaton of a statistical hierarchical framework to model the relationship between biodiversity and environmental drivers and pressures.

The data in each case study presented specific issues concerning sampling methodology, regularity of sampling and misalignment of the response data with the available environmental covariates. The analyses highlighted important issues in sampling techniques including the sampling methodology, scale of response, calculation of biodiversity, alignment of covariates and response. This chapter will give an overview of the analyses performed, the inferences made from these results, and evaluation of the developed frameworks. Furthermore, possible avenues of further framework development will be discussed for future analyses.

6.1.1 Macrophytes

Loch Leven was the setting for the initial case study in chapter 2, where data from the submerged macrophyte community since 1905 were used as the response. The analysis involved ascribing changes in the macrophyte community to changes in the environmental state of the shallow lake. Previously, work conducted on this particular lake has usually focussed on the maximum growing depth (MGD) of the macrophytes as a response had inferred the impact of nutrient loading by reference to the witnessed changes within the macrophyte community in the lake. The task undertaken here was to explain the variability in the biodiversity of the submerged macrophytes using both the total phosphorus load and MGD.

Initially, an ordinary linear model was used to model the lake taxon richness response, since early survey data did not record the taxon presence within each sample. This simple model fitted using a very sparse dataset showed the MGD of macrophytes, which is indicative of the lake water quality, to have a positive correlation with the lake taxon richness. This led to the taxon richness of individual drag-rake samples being modelled with a subset of the available surveys, using a Poisson distribution to fit a Generalised Linear Model (GLM). Though only the four most recent surveys could be utilised in this model, a similar relationship was obtained to that in the lake taxon richness model; the MGD had a significant positive effect on taxon richness and this was the same effect in all sectors across the lake. Using a Generalised Linear Mixed Model (GLMM), the random effects of Year and (lake) Sector within Year allowed the variability within and between years and within years, between regions of the lake to be estimated. Given that the MGD was included in all three selected models, this provides evidence that this is a consistent effect. The uncertainty associated with the covariance function fitted to the model residuals indicated that the spatial correlation between sectors of the lake is very low.

In summary, the analyses in this chapter show the positive correlation between the MGD of the macrophyte community and the macrophyte taxon richness, concurring with previous studies, such as Vestergaard and Sand-Jensen (2000). MGD is considered to be representative of the trophic status of the lake, given it is a measure of the area colonised by the macrophytes. Not all taxa observed in the lake at the beginning of the 20th century were observed in the later surveys, but as the MGD has increased in the last 30 years, the observed macrophyte taxon richness at two scales has increased, indicating a recovery from eutrophication over this period. This result concurs with research conducted by May and Carvalho (2010) at Loch Leven itself and Sand-Jensen et al. (2008) at Lake Fure in Denmark, that macrophyte taxon richness is dependent upon the MGD and thus trophic status of the lake.

6.1.2 Carabids

In contrast to the macrophytes which were sampled from a single lake, the beetles as analysed in chapter 3 were modelled at 10 rural sites, sparsely situated across Great Britain. The beetle response was an index calculated from the numbers of carabid genera caught in pitfall traps. Therefore the response is based on the activity density of the various taxa, which is a surrogate measure of the carabid population. Two indices were used on these aggregated values: log total number of beetles and the Shannon diversity index. Meteorological, biogeochemical and aggregate habitat data were used as environmental covariates, with Year fitted as a linear effect. The Month effect was fitted as a categorical effect and as random in respective exploratory models; it was decided to fit Month as categorical in the models tested.

Initial exploratory models for all ten sites of the response data at the Site and Year level were fitted as well as in a separate model at the Transect and Year level. In this way, the temporal scale of covariate and response data is the same and the three transects are each site are treated as independent.

Initially, two sites with very different responses were analysed separately, in order to assess the best response to be used in a multi-site model: Rothamsted in southern England and Sourhope in southern Scotland. Both models of the Rothamsted site showed temperature, nitrogen deposition and month to be significant covariates. In the model for Sourhope, the same covariates were included in the final models for the Shannon index and log total: temperature, month and year. Using responses from all ten sites showed temperature, wind,

nitrogen deposition and month to be included in the Shannon model and temperature, month and year in the log total model. The positive response of the log total to temperature concurred with previous studies. The negative log total response to nitrogen deposition was in contrast to previous studies (Raworth et al., 2004; Batáry et al., 2008). However, the pressure of nitrogen deposition was two orders of magnitude lower in the ECN, and thus the observed response may be the result of smaller-scale changes or a spurious correlation.

Temperature was observed to have a positive effect in all final models apart from in the Rothamsted log total model. This general result concurs with previous studies which assessed the response of carabid to temperature changes (Honek, 1997; Saska et al., 2010). Given that Month was included in all final models, the effect of Temperature is inferred to be in addition to the seasonal trend of beetle activity.

The large amount of residual variance from the null models left unexplained by the model covariates, it is not clear what environmental drivers and pressures are affecting the changes in the beetle population. This could be due partly to the lack of ground-truthed covariate data. Furthermore, the coarse variability in the covariates and the fine scale of beetle response meant that since the explanatory and response variables were not measured on the same scale, it was more difficult for the fine-scale changes in the response to be explained by the environmental drivers and pressures. There are other possible reasons for the unexplained variability, including complex interactions between carabid prey, predators as well as between carabid species. There is also the possibility that random noise in present in the data; that numbers of beetles caught can fluctuate when individuals do not fall into a pitfall trap, rather than because of an biotic or abiotic impact.

With regard to the site and transect random effects in the multi-site model, the variability between transects was not as much as between sites. This indicates that transects at the same site showed more similar responses with each other than with those transects at other sites. The autocorrelation is estimated to be higher in the log total model than the Shannon index model. This may be due to the presence or absence of rare taxa may altering the Shannon index, but not the log total of individuals (Neher, 2001).

Given the capacity for beetle numbers to vary greatly spatially and temporally (Saska et al., 2008), it is not unsurprising that a large amount of variability in the response is unexplained

in the final models. The variability may be the result of land management effects not taken into account in this analysis. Further site-specific knowledge may be necessary to understand what is occurring at each site and within each transect.

6.1.3 Plant biodiversity and environmental pressures

The Countryside Survey provided biodiversity data from three field surveys, which were analysed in chapter 4. Indices were calculated for each survey plot from the percentage of the plot covered by each species present. The three most recent surveys were used in the analysis, from 1990, 1998 and 2007. A Generalised Additive Model structure was used initially in this analysis, affording greater flexibility in the relationship between the model covariates and the response than a Generalised Linear Model.

Models were fitted for each of the eight most common habitats separately using data from all three surveys as the response. Four different response measures were tested: Total species richness, Simpson's Index of Diversity, Shannon index and Smith and Wilson's E_{var} index. The arable sites were removed from the analysis at this point as there was deemed to be too much variability in the biodiversity response as a result of land management, leading to poor model results. The Shannon index was chosen as the response for a model of the remaining seven habitats, as the deviance explained was relatively good compared with the other responses and the diagnostic plots associated with the single habitat Shannon models showed no violation of model assumptions.

The resultant model of seven habitats showed different responses in biodiversity to nitrogen deposition and rainfall covariates respectively. These models showed the variability in the biodiversity of the sampling plots to be driven by rainfall and nitrogen deposition in the 1998 model, and habitat, Easting and Northing in both 1998 and 2007 models. In the 1998 model negative correlations with nitrogen deposition are observed for four of the seven habitats, with two of these habitats, Broadleaved, Miyed and Yew Woodland and Coniferous Forest, having significant coefficients. The nitrogen relationships with Improved Grassland and Neutral Grassland are positive and significant. Given recent literature has highlighted the negative impact on species richness of increases in nitrogen deposition, e.g. in acid grasslands (Stevens et al., 2010), these positive relationships for a single survey should be analysed more closely in order to to understand the relationship between nitrogen and the Shannon index.

In encountering the problem of misalignment between environmental covariates and the model response in all three case studies, a hierarchical model was developed in the third and final case study, in order to realign the covariates to the response positions before inserting their predicted values into the biodiversity regression model.

Data realignment

In order to realign the covariate data, a method is developed to regress the rainfall and nitrogen deposition values against altitude for gridded square data in a small region around each CS site, which would allow those covariates to be predicted at each CS plot using the precisely known altitude. This method would also also the uncertainty associated with the predicted values by sampling an error term from the prediction distribution. In order to perform this realignment and error estimation, a statistical downscaling technique known as Perfect Prognosis was adapted. By repeatedly sampling this error term and each time fitting the biodiversity model with the sampled covariates, the mean AICc value of the fitted models can be calculated and compared against other tested models as in other analyses.

A simulation study was set up with a rainfall covariate, in order to compare the biodiversity model performance of the downscaled and non-downscaled covariate models, as the within-square and between-square variability was altered. When there is a correlation coefficient of around 0.95 or higher between rainfall and altitude at the coarse-scale, i.e. across the 15×15km region surrounding the CS site, the model fitted with downscaled data performed better than the non-downscaled model. However, as the between-square variability increased, a negative bias was observed in the coefficient estimates of rainfall. The non-downscaled model showed no bias in the rainfall coefficient,but was less precise.

On the basis of this simulation, the necessary correlation between the covariate to be downscaled and the predictor covariate was estimated; a correlation of 0.95 is required in order that the downscaling methodology improves the biodiversity model performance. Both the rainfall and nitrogen deposition values showed weak correlation with altitude for the regions of interest and it was inferred that they should not be downscaled, given the available data.

6.2 Main conclusions

This thesis has highlighted several important issues in the realm of biodiversity modelling: the DPSIR policy tool, sampling methods, biodiversity indices, scale and model framework will be discussed with reference to the analyses conducted.

6.2.1 DPSIR

The DPSIR framework was introduced initially as a policy tool to aid understanding of the impact of environmental drivers and pressures on the environment. Such a mechanistic framework is difficult to implement; a hierarchical system linking drivers with pressures and subsequently to states and impacts could be created, but such a method may be very complex. In these analyses, the biodiversity response was modelled with regard to explanatory covariates, which could be measures either of environmental drivers, pressures or states.

Given this method of modelling, matters arising from the DPSIR concept were discussed before and after the analysis, rather than imposing the DPSIR framework upon the model. In this way, possible covariates are then chosen for use in the model prior to fitting the structure; after obtaining the chosen model, inference can be made as to the relationship between the remaining model covariates and the biodiversity response with regard to DPSIR. If data are to be collected specifically for a DPSIR framework, the sampling scheme should be set up with this concept in mind, which would allow easier implementation.

6.2.2 Sampling

The response data in each case study were taken from long-term monitoring projects. The Loch Leven data were irregularly collected and not always with the same degree of precision as to the location of each datum. The carabid and CS datasets, having been sampled using the original methodology continuously, were more easily adapted into set model frameworks. The continuity of sampling methodology is therefore of utmost importance. If the same methods are used in repeatedly sampling the same sites and precise information as to the time period and location of sampling is recorded, trends in the biodiversity of species communities can be more easily identified, given the identical techniques used in collecting and recording the data. Both the carabid and CS repeated samples were conducted at the same locations

throughout time. The Loch Leven analysis was hindered as a result of the lack of repeated sample locations and regular comprehensive surveys.

6.2.3 Biodiversity indices

Several different biodiversity measures were used in the analyses; the information provided by each index was accordingly different. However, the indices tested showed a good degree of correlation in many cases. The inferences made on the spatio-temporal changes in biodiversity are partly dependent upon the biodiversity index response used. In turn, the choice of diversity index used is itself often dependent on how the data were first measured.

As discussed initially in chapter 1, not only do certain biodiversity measures give different information about the species community being modelled, they also depict the data in ways that fit certain distributions better than other indices. The difficulty in modelling using Simpson's Index of Diversity and Smith and Wilson's E_{var} index is that they produce values on the range $[0,1]$, with clustering at both bounds of the range. In the context of the beetle data the Shannon index was chosen, since its range is $[0,\infty)$, and there is relatively less clustering of values at zero obtained. The benefit of using the Shannon index was not only the reasonably high correlation exhibited both with the Simpson and E_{var} indices for a large proportion of the data. It was also the best-fitting of the indices for the CS data when modelled using a GAM distribution. The Loch Leven data were considered insufficient for using any index other than taxon richness, since abundance or mass within each observed sample was not recorded. In the case of the carabid analysis, the log total and Shannon indices tested showed slightly different relationships with the covariates; this is not unlikely, given that the log total is species-invariant and the Shannon index is sensitive to rare species.

In light of the use of several biodiversity indices, the complete biodiversity of a community cannot be fully explained by reference to a single univariate measure; only a facet of the community dynamic can be viewed. A univariate measure of a specific taxon group does not allow complete understanding of the dynamic of a specified taxon assemblage. Indices of macrophyte, carabid and plant communities do not give the whole picture of the environment or habitat which they represent. Many other important taxon groups are present within a single habitat, which interact with the assemblage of interest. The results of bird or butterfly studies, as referenced in chapter 3 may need to be assessed in conjunction with these results, in order to make appropriate judgements about the overall condition of that habitat.

It is difficult when analysing biodiversity as measured by an index, to make direct inferences as to the effect on a population. Thus, any inference made on the impact of a certain covariate on a given biodiversity response is not necessarily an end in itself, but cause for further research of a particular community of species. Impacts identified in such examples as given in this thesis are indications of the need for closer study of their precise effects. In so doing, the vital functions of ecosystems can be preserved and the services necessary to humanity can be maintained.

6.2.4 Scale

This thesis contains three case studies of biodiversity modelling, each with different resolutions at which the explanatory and response data are measured or estimated with different challenges involved in the modelling of the data. The recurring issue witnessed is the question of how best to combine multiple sources of information in a modelling framework. The Loch Leven analysis involved the delineation of sample taxon richness into lake sectors in order to identify the variability in sample taxon richness across the lake. In this case, a clearer understanding of spatio-temporal change in macrophyte richness is gained when the response data are separated accordingly.

In the tested models, the carabids were aggregated spatially and temporally to the transect and month level, showing the benefits of obtaining a sensible model that can be gained by such a process at the loss of fine-scale information, since this was also the spatio-temporal resolution at which the covariates were available. The response could have been aggregated to the site level also, but given the transects were considered to be independent beetle communities, such an aggregation was deemed unsuitable.

The case study on the Countryside Survey involved the most complex of these issues, since in this analysis the hierarchical model framework was developed, which involved developed a method to downscale covariates to the CS plot level. Both covariates were modelled at the centroid of their associated grid squares and there is unknown variability in these two covariates over short distances. Having used the explanatory covariates as they were available in a generalised addtitive model structure, a much simpler simulation using a linear model was created. The use of this method was not considered suitable for the data at hand, due to the weak correlation between the respective covariates and altitude.

If a dataset can be modelled at more than one scale, such as the macrophyte data or the carabid data, obtaining similar trends in the analyses can be a good sign that the effect is present and not merely spurious. If not, the choice of scale should be made prior to analysis and not with respect to the desired result which has been obtained at a certain scale.

6.2.5 Environmental impact

Here, the impacts of environmental drivers and pressures identified in the case studies are discussed. Given the significance of environmental covariates in describing the variability in the biodiversity responses, inferences can be made about their impacts.

Relationships are found between environmental covariates and the biodiversity response in all three analyses. The results of the Loch Leven study showed the recovery of the macrophyte population, as evidenced by the increase in taxon richness since 1966. The pressure of elevated levels of nutrient loading to the lake had been identified by May and Carvalho (2010) as impacting upon the MGD of the lake macrophytes. The estimated loading of total phosphorus from each tributary stream would allow testing of the hypothesis that the location of TP loading to the lake affects the taxon richness of the macrophyte population.

The MGD of the macrophytes recorded within each lake sector may also help in explaining the spatial variability in the recovery of the macrophytes. Changes in the abundance of individual fish and bird species and their position in the lake system over time may also help in understanding these changes. In the carabid models, predator populations such as rodents or birds could be used in modelling larger ecosystem processes.

In the context of the beetle populations, temperature and nitrogen deposition were included in many of the final models. Whilst the effect of temperature showed agreement with previous studies (Honek, 1997; Saska et al., 2010), the effect of nitrogen deposition appeared in contrast to studies on the effect of fertilizer application on beetles (Raworth et al., 2004; Batáry et al., 2008). Although nitrogen deposition is two orders of magnitude smaller than the nitrogen content in fertilizer applications, the reason for this reversal of the effect is not understood. The negative effect of temperature at Rothamsted is also unclear and requires closer analysis as to other possible pressures which could have caused this perhaps spurious correlation.

There is still a large amount of variability in the observed response which was not described by the chosen environmental covariates. The large percentage of unexplained deviance in the carabid models could be due to a number of reasons. Firstly, only a small number of environmental covariates were considered. Also, lagged variables were not tested either, and so the potential impact of non-contemporaneous environmental covariates was not assessed. Due to the small number of sites it was difficult to gain a complete picture of how carabid diversity is affected by the environment within Great Britain as a whole.

In both the carabid and CS analyses, some of the covariates such as nitrogen deposition contain several different molecules, which have been cumulatively estimated. Nitrogen and sulphur deposition estimates could be separated into the estimated deposition of each of their contributing compounds. The specific estimates of different nitrogen compounds deposited would aid in identifying the impact of certain molecules which have a greater impact on the diversity response than others. The estimated deposition of other nutrients could be used as covariates in the modelling process, such as phosphorus. Thus the associated pressures impacting upon biodiversity could be isolated. Population information from the surrounding region would help in inferring if nearby human activity was a driver of change in the diversity. Arable habitats may be subject to wide variation in fertiliser addition and so have very different inputs of nutrients to their individual systems.

The given habitat was a good descriptor of the plant biodiversity in the models of CS data. Spatial location was also significant in nearly all models, as fitted using a joint smoother of Easting and Northing position, indicating biodiversity in plant populations may also be a result of the distribution of individual species, which are dependent upon inter-species competition.

The effect of nitrogen deposition has been widely studied (Stevens et al., 2004; Smart et al., 2005; Stevens et al., 2010; Tipping et al., 2013), but the responses observed in the CS models varied by habitat greatly. Understanding the role of nitrogen in individual habitats is key to understanding the observed effects in such models. It is however difficult to estimate the effect that the rainfall and nitrogen deposition covariates have upon the biodiversity response in chapter 4 without accurately estimating the error in the calculation of the rainfall map or the within-square variability. A certain habitat where there appears to be a relationship between the Shannon index and rainfall is in the Coniferous Forest habitat; this effect may

need to be studied more closely, in order to look at the spatial pattern of diversity in this particular habitat.

Variability in the biodiversity as measured by the Shannon index is not described particularly well by the covariates available. A much larger percentage of deviance in the 1998 CS data was explained by the final model than in the 2007 CS data. This means either that the model was not complex enough to explain the variability fully, did not include all relevant covariates, or enough information on those covariates which were included.

There is a large amount of unexplained variability in all three case studies, indicating that the biodiversity as measured by the indices used is dependent upon other external or intra-community forces. Alternatively, the model covariates which were included in the models tested were not accurate enough.

6.3 Additional development

In light of the highlighted case studies in this thesis, there is potential for further analysis in many areas of ecological modelling which have been discussed. Possible avenues of further research are given below.

6.3.1 Sampling

When sampling biodiversity, the location and time of each measurement should be precisely recorded. In the macrophyte sampling, repeated samples at the exact same locations were not made. If they were, the coincidence was not recorded. In order to assess the change in sample taxon richness at specific locations, drag-rake samples need to be co-located with those samples made in previous years. GPS measurements were made of the location of drag-rake samples in the 2008 survey and could be compared against future surveys. Furthermore, a map of the spatial distribution of macrophyte taxon richness could be created. The spatial correlation of the sample taxon richness could be estimated more easily using this information. GPS measurements are subject to a certain degree of error and this would have to be taken into account in the modelling process. However, if the starting position and

direction of each transect were known, less spatial error between sampling positions may be incurred.

Reducing sampling bias is important in biodiversity modelling, in order to avoid selecting one area for observation over another because it might yield more attractive results. Whilst there are no zero observations in the macrophyte data from Loch Leven, there is no reason to suggest that the position of the transects was chosen so that a higher taxon richness would obtained.

As already noted, the beetle measurements within each transect for a defined sampling fortnight can have high variability. In order to compare the spatial variability of beetles beyond the range of a certain transect traps could be set up in a grid formation. This would allow a better understanding of the movement of the beetle community across the region of interest.

With regard to the CS methodology of survey, the sites have up to 60 plots sampled within each $1km^2$ region. All but five of these plots are specifically positioned, in order to sample a certain locale such as a streamside, road verge or hedgerow. While such targeted plots are important to understanding specific processes in these areas, the randomly located plots are most valuable, when estimating within site variability.

In these and in many other environmental studies, a complete census of the population rather than a sample is not only impractical, it would be highly disruptive to the ecosystem. In the same way, measuring all environmental covariates at all sampled sites is infeasible. Thus, complete understanding of the community dynamic at all positions cannot be obtained. Different study taxon groups or goals demand different sampling regimes (Buckland, 2009). It is important to ascertain what the aim of a long-term sampling scheme is before starting to sample the population.

6.3.2 Biodiversity indices

Having performed downscaling of environmental covariates to the plot level in the CS analysis, a different challenge would be upscale the biodiversity variable. This allows a broader

view of the response but detail on individual communities may be lost. Species accumulation curves are similar tools used to perform extrapolations of species richness, as conducted by MacArthur and Wilson (2001). In sampling only 5 randomly located 200m^2 plots in each 1km^2 site, only 0.1% of the whole site area is randomly sampled. Upscaling the diversity from a sampled area totalling 1000m^2 to 1km^2 is a large extrapolation, and would incur a great deal of error. Use of the other non-randomly located plots in this process may help to obtain a more accurate upscaled prediction. Habitat covariate data would need to be aggregated, were sampled plots to be aggregated in this manner.

As commented upon earlier in section 1.3, when investigating the biodiversity of a community, the index chosen can either inform about the evenness or the heterogeneity of the taxon community, or some combination of the two. The measure chosen for analysis has to be from a fixed position between richness and evenness by calculating the diversity using a defined index. Such univariate indices cannot therefore give perfect information as to the value of both these extreme positions.

Possible measures not investigated in this thesis include composite indices of the relative abundances of the species, as developed by Buckland et al. (2005). The recent emergence of work on diversity profiles of communities has been conducted by Jost (2009, 2010) and Leinster and Cobbold (2011), which show the manner in which the evenness and heterogeneity of communities can be viewed along a continuum . Taking evenness and heterogeneity as the two extremes on this continuum, it is shown how other indices lie on this continuum. This is formed using the Hill numbers, a system which defines the relationship between certain diversity measures, first proposed by Hill (1973). The ath Hill number, for a community of n taxa with taxon i having a proportion of p_i, is defined as:

$$H_a = \left(\sum_i^n p_i^a \right)^{\frac{1}{1-a}} \tag{6.1}$$

where H_0 is taxon richness, sensitive to rare species, and H_∞ is the reciprocal proportion of the most common taxon, insensitive to rare species. By integrating over a from 0 to infinity, a continuous measure of diversity is formed: a diversity profile with a univariate value. This new index could be modelled in a similar manner to the methods used in this thesis, allowing the univariate response to reflect the magnitude of diversity of the population of interest, while not needing to give weighting to either evenness or heterogeneity.

6.3.3 Scale

In contrast to the macrophytes, the carabid populations were sampled at several different sites for approximately half the year and information on the spatio-temporal variability in the covariates was readily available. This allowed a greater complexity in the modelling structure. However, many of the covariates were from model estimates. Reliable measured data at each transect or site location would help in the accurate estimation of the relationships with the response and increase the percentage of deviance explained. Rainfall, nitrogen and sulphur covariates could be downscaled to the transect or trap level in the same way that the CS covariate data were downscaled.

6.3.4 Model framework

The low percentage of null model residual deviance explained by the models in all three case studies highlight the need to try and identify the cause of the remaining variability. Not only could different covariates be assessed, but also estimation of the covariate uncertainty both spatially and temporally could be made.

With regard to further work on the hierarchical model, a multivariate downscaling model could be created to jointly model rainfall and nitrogen, in a similar fashion to Berrocal et al. (2010). Since a large proportion of nitrogen deposition is comprised of wet deposition, the level of nitrogen deposition estimated at a certain point is dependent upon the rainfall that falls there. Different sources of data could be included in calculating the uncertainty of rainfall and nitrogen deposition values. Information on the probability of extreme events could be included, such as flooding or drought for rainfall.

The region over which the local regression for downscaling was fitted could be increased in order to obtain a more general spatial relationship between the covariate to be downscaled and the predictor. The 15×15km grid proposed for the rainfall data could be extended. In different analyses, there may be good reason for the enlargement of this local regression, such as the estimated transport distances of certain emitted pollutants or the extent of the orographic effect in a given region. The prediction step of the downscaling stage could include finer-scale altitude data and in addition other predictor variables could be included such as aspect, gradient and information on cloud cover. The canopy structure of the habitat

could also be used in this process. This may reduce the standard error associated with each predicted covariate value, thus reducing the prediction distribution variance. When a large amount of between grid square variability for nitrogen deposition or rainfall exists at a given CS site, the model estimates should be ground-truthed, rather than inserting data with large uncertainty attached into the model.

In modelling plant communities, information on the soil is important also. Thus the actual nitrogen available to the plant could be calculated using a partially mechanistic model. The calculated availability of nitrogen would be subject to the value of the nitrogen deposition estimated values at the response locations and their associated uncertainties. Therefore another level of modelling could be accommodated into the hierarchical structure.

Research in the area of downscaling and covariate uncertainty is prevalent within ecological modelling. Malone et al. (2012) describe and implement a general downscaling technique to produce a soil organic carbon (SOC) map for an area of Australia. In downscaling from the 1km grid to the 90m grid resolution, data from a digital elevation map is used to predict SOC using a weighted generalised additive model. The mean of the downscaled predictions within each 1km square are restricted to be equal to the associated coarse 1km grid value. The uncertainty associated with the downscaled values is not, however, estimated.

Work by Foster et al. (2012) has used a Berkson error framework on misaligned data to assess the bias caused by covariate uncertainty in a ecological context. Using a case of misaligned data from the Great Barrier Reef, a Berkson measurement error model is proposed to counter the simulated problems and a study is used to illustrate the potential difference in inferences made in the resultant model.

6.4 Final conclusions

The development of these statistical models for these particular datasets is not designed to be exhaustive, or suitable for all similar data sources. The hierarchical framework was developed in the light of the problem of covariate uncertainty that was faced, where the

realignment of model covariates led to intra-square uncertainty being estimated using local variability.

Many different analyses involving fine-scale environmental data could benefit from uncertainty estimation, similar to the downscaling method described in this thesis. Models such as MultiMOVE which seeks to model habitat suitability for plant species as outlined by Rowe et al. (2011) could incorporate such methods into their frameworks relatively simply. The extension of this downscaling method beyond ecological frameworks, to hydrological and epidemiological impact studies is also foreseeable, since the biodiversity response is not a necessary precursor to the justified downscaling of covariates.

The issue of data misalignment is often simply ignored in statistical modelling. If covariate data encompasses the response region, the data are considered to be co-located with the response. Covariate uncertainty should not be discounted, if taking account of it can have consequences for the model result and the inference that can be made from these results. The potential implications of fine-scale downscaling using a similar hierarchical model are far-reaching and could benefit subsequent analyses in many different areas of spatial modelling. Careful selection of the predictors will lead to precise realignment, accurate uncertainty estimation and improved model results.

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